The Douvilleiceratidae (Ammonoidea) of the Lower Aptian historical stratotype area at Cassis-La Bédoule (SE France)

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Abstract: Recent biostratigraphic research in the marly limestones of the Cassis-La Bédoule area (SE France) provided a rich macrofauna of Douvilleiceratidae PARONA & BONARELLI, 1897. From the uppermost Barremian (*Pseudocrioceras waagenoides* Subzone) to the middle Aptian (*Parahoplites melchioris* Zone), specimens of *Prochelonicera*s, *Cheloniceras*, *Roloboceras*, *Megatyloceras* and *Epicheloniceras* were collected in succession. In this paper we describe the various genera and species from this material and delimit precisely their stratigraphic positions. Our study shows that each genus or subgenus characterizes a discrete stratigraphic interval. In addition, the *Cheloniceras meyendorffi* (upper Bedoulian), *Epicheloniceras debile*, *Epicheloniceras gracile*, and *Epicheloniceras buxtorfi* (Gargasian = middle Aptian) subzones, originally defined in England by CASEY (1961a), are identified for the first time in the Lower Aptian stratotypic area of Cassis-La Bédoule.

Key Words: Cretaceous; Aptian; ammonites; Douvilleiceratidae; taxonomy; biostratigraphy.

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Résumé : ***Les Douvilleiceratidae (Ammonoidea) de la région du stratotype historique de l'Aptien inférieur à Cassis-La Bédoule (SE de la France).-*** Des recherches biostratigraphiques récentes dans les sédiments barrémo-aptiens du secteur de Cassis-La Bédoule (SE de la France) ont révélé une riche macrofaune de Douvilleiceratidae PARONA & BONARELLI, 1897. Du Barrémien terminal (Sous-zone à *Pseudocrioceras waagenoides*) à l'Aptien moyen (Zone à *Parahoplites melchioris*) nous avons recueilli, de bas en haut, d'abord des spécimens de *Prochelonicera*s, puis de *Cheloniceras*, *Roloboceras*, *Megatyloceras* et *Epicheloniceras*. Dans cet article nous décrivons et situons stratigraphiquement les différents genres et espèces de ce matériel. Notre étude montre que chaque genre ou sous-genre caractérise un intervalle stratigraphique particulier. De plus, les sous-zones à *Cheloniceras meyendorffi* (Bédoulien supérieur), *Epicheloniceras debile*, *Epicheloniceras gracile* et *Epicheloniceras buxtorfi* (Gargasien = Aptien moyen), définies à l'origine par CASEY (1961a) en Angleterre, sont reconnues pour la première fois dans la région stratotypique de l'Aptien inférieur de Cassis-La Bédoule.

Mots-Clefs : Crétacé ; Aptien ; ammonites ; Douvilleiceratidae ; taxinomie ; biostratigraphie.

1. Introduction

In recent decades several zonal and subzonal schemes based on ammonites have been proposed for the subdivision of the Barremian-Aptian interval, such as those of CASEY, 1961a (South England); BOGDANOVA, 1971 (Turkmenistan); RAWSON, 1983 (Corre-

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lation of French, English and North German Aptian zonal schemes); KOTETISHVILI, 1986 (Georgia); DELANOY, 1997 (Vocontian Basin); MOULLADE *et alii*, 1998 (Lower Aptian stratotype at Cassis-La Bédoule); ROPOLO *et alii*, 2000, 2006 (Lower Aptian stratotype); DAUPHIN, 2002 (Vocontian Basin). Based on these works, progressively updated schemes have been retained for the Mediterranean Region by the IUGS working groups (HOEDEMAEKER, BULOT *et alii*, 1990; HOEDEMAEKER, COMPANY *et alii*, 1993; HOEDEMAEKER, CECCA *et alii*, 1995; HOEDEMAEKER, RAWSON *et alii*, 2000; HOEDEMAEKER, REBOULET *et alii*, 2003; REBOULET, HOEDEMAEKER *et alii*, 2006). The present consensus, still provisional and in the form of recommendations, is as follows:

- Uppermost Barremian: heteromorphic ammonites, such as *Martelites sarasini* and *Pseudocrioceras waagenoides*, are chosen as species-index.
- Lower and middle Aptian: representatives of three families (Deshayesitidae, Douvilleiceratidae and Parahoplitidae) are used as markers of zones, subzones or horizons. The Deshayesitidae are considered as the characterizing group for all the main subdivisions of Lower Aptian. Thus, the recent revision (ROPOLO *et alii*, 2006) of the Lower Aptian historical stratotype of Cassis–La Bédoule (SE France) has led to an identification and description of the species and the precise delimitation of the stratigraphic position of all the Deshayesitidae collected there, and also a proposal for a zonal subdivision using the succession of the *Paradeshayesites oglanlensis*, *Paradeshayesites weissi*, *Deshayesites deshayesi* and *Dufrenoyia furcata* zones. Accessorily, a *Roloboceras hambrovi* horizon has been recognized in the middle part of the *Deshayesites deshayesi* zone, just below a *Paradeshayesites grandis* subzone.
- the Barremian/Aptian boundary is placed at the FAD (first appearance datum) of the genus *Deshayesites* and the Lower /middle Aptian boundary is defined as being at the upper limit of the *Dufrenoyia furcata* Zone.

To characterize the Lower and middle Aptian zones even better and to complete the description of the faunal content of the Cassis-La Bédoule type-area, in this paper we describe and locate stratigraphically the populations of Douvilleiceratidae that occur in the Bedoulian together with representatives of the genus *Deshayesites*, as well as the Douvilleiceratidae which are also found in the Gargasian. We thus study in detail the genera *Procheloniceras*, *Cheloniceras*, *Epicheloniceras*, *Roloboceras* and *Megatyloceras*. Changes in the sub-zonal boundaries are proposed on the basis of new discoveries of specimens of Cheloniceratinae collected *in situ*. These additional data are of major importance for a more thorough definition of the Lower and middle Aptian biostratons and make correlations between the Tethyan and Boreal realms easier.

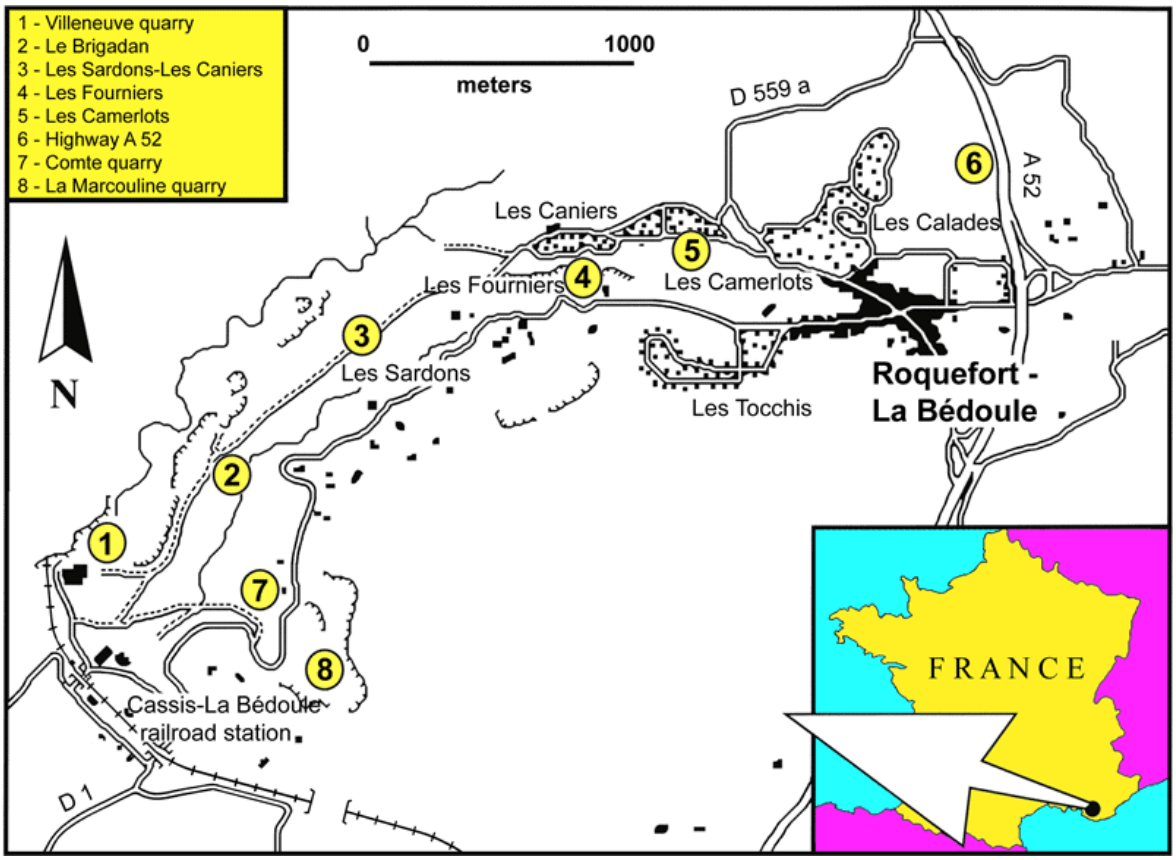


Figure 1: Location of the studied sections in the Cassis-La Bédoule area.

2. Biostratigraphy

2.A. Faunal data

Five sections were investigated in the vicinity of Roquefort-La Bédoule (Les Caniers, Les Fourniers) and Cassis (Le Brigadan, Comte quarry, La Marcouline quarry) (Fig. 1). These outcrops made it possible to build a continuous composite section that includes strata ranging in age from Late Barremian to late Gargasian, with the exception of the Bedoulian/Gargasian transition (see below).

The material collected spans a time interval which includes the Late Barremian Sarasini Zone, the Early Aptian Oglanlensis, Weissi, Deshayesi, Furcata zones and the middle Aptian Martini and Melchioris zones.

Our record shows that three faunal intervals can be clearly identified in the stratotype area on the basis of the distribution of the Douvilleiceratidae (more particularly the Cheloniceratinae):

- a *Prochelonicera*s level (beds 46 to 121 in the Cassis-La Bédoule railway station section) including the main part of the Waagenoides Subzone, the Oglanlensis and the Weissi (*pro parte*) zones. In this interval, we collected several species of *Prochelonicera*s: *P. pachystephanum* (Uhlig, 1883), *P. albrechtiaustriae* (Hohn. *in* Uhlig, 1883), *P. stobieskii* (d'Orbigny, 1850) and *P. dechaux*i (Kilian & Reboul, 1915) (Figs. 2-3).
- a *Cheloniceras* level (beds 144 to 178 in the Cassis-Comte quarry section and beds M3-M8 in La Marcouline quarry), which comprises the late Bedoulian Deshayesi and Furcata zones and the lowest beds of the middle Aptian. The following species were collected: *Cheloniceras seminodosum* (Sinzow, 1906); *C. kiliani* (Koenen, 1902); *C. mackesoni* Casey, 1961; *C. cornuelianum* (d'Orbigny, 1841); *C. parinodum* Casey, 1961; *C. crassum* Spath, 1930; *C. meyendorffi* (d'Orbigny, 1841); *C. disparile* Casey, 1961; *C. minimum* Casey, 1961 (Figs. 3-5).

  Within the Deshayesi Zone is included a *Roloboceras/Megatyloceras* interval (beds 148 to 170 at Cassis-La Bédoule), with *Roloboceras hambrovi* (Forbes, 1845); *R.* gr. *transiens* (Casey, 1961); *R. horridum* (Spath, 1930); *Megatyloceras ricordeanum* (d'Orbigny, 1841); *M.* aff. *coronatum* (Rouchadze, 1933).

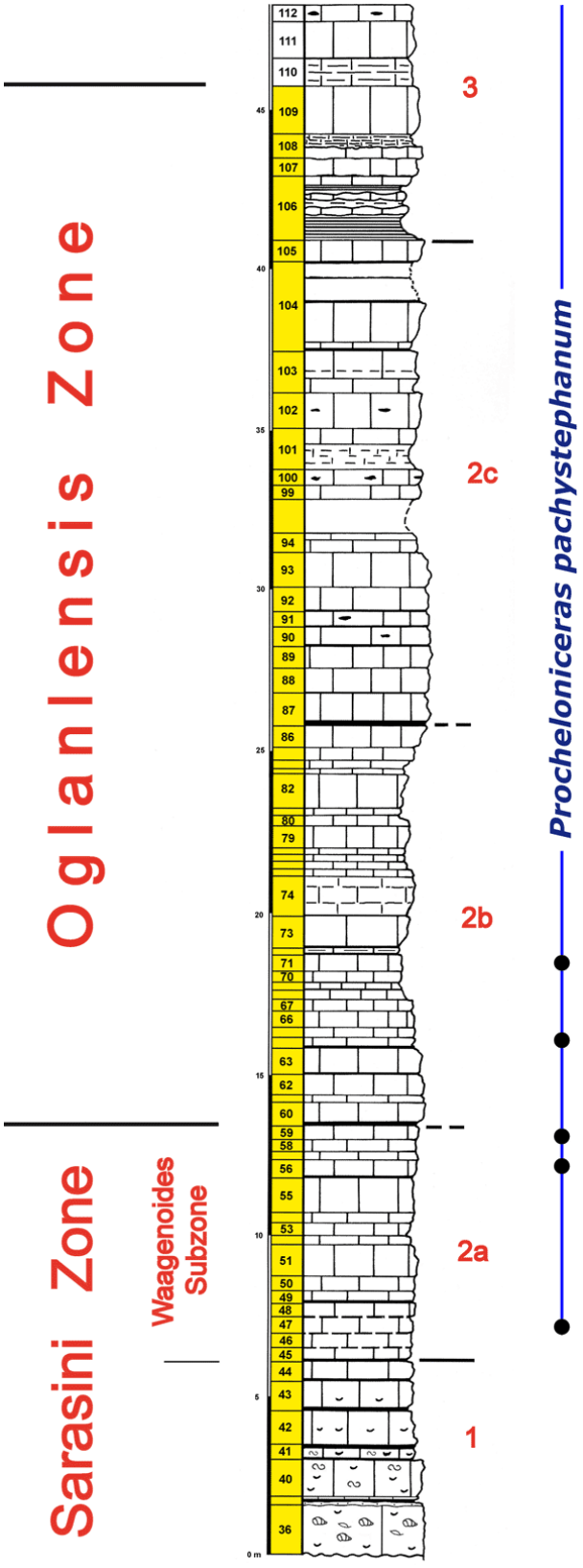


Figure 2: Uppermost Barremian / Lower Aptian (*pro parte*) composite section of the Cassis-La Bédoule area with the stratigraphic position of the collected Cheloniceratinae.

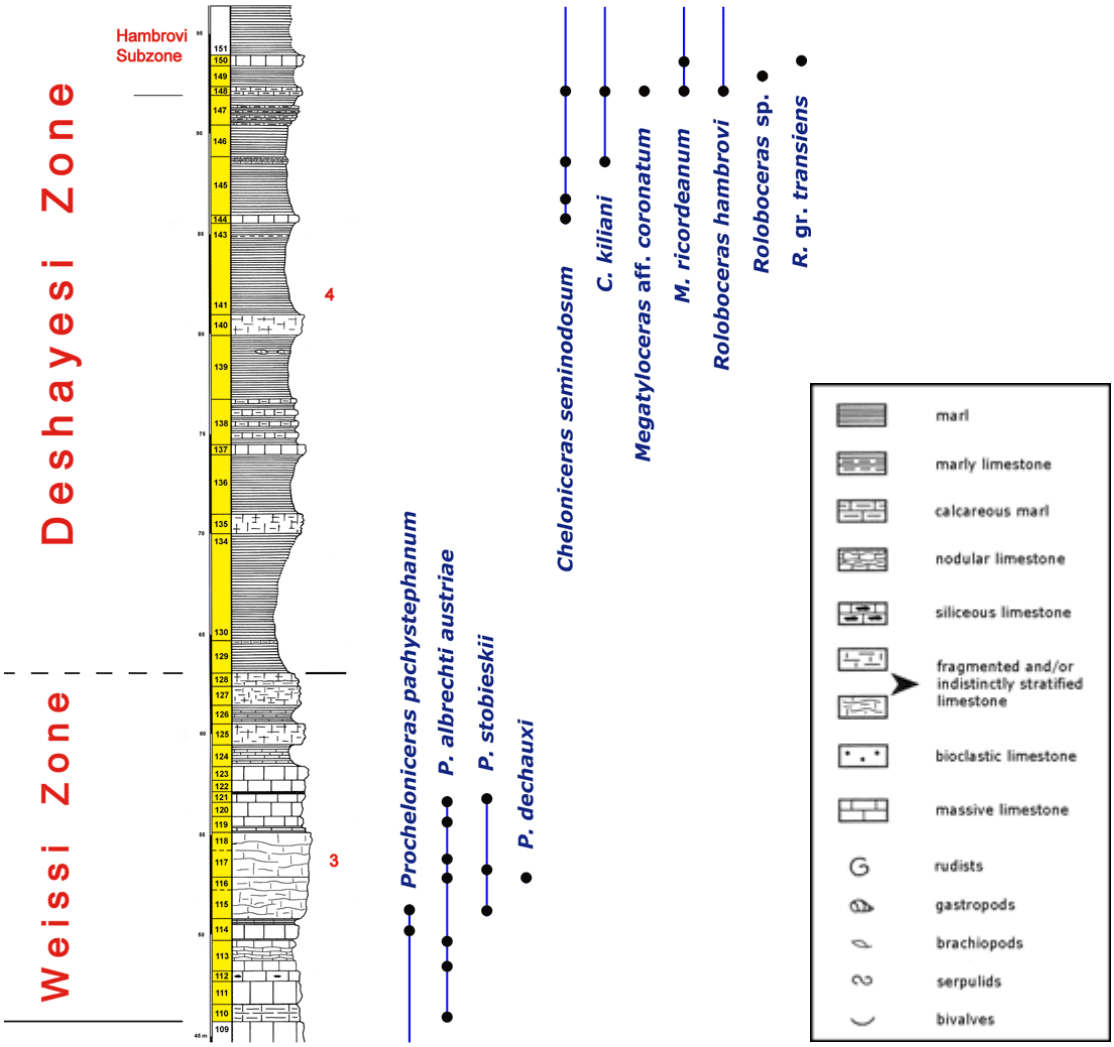


Figure 3: Lower Aptian (*pro parte*) composite section of the Cassis-La Bédoule area with the stratigraphic position of the collected Cheloniceratinae and Roloboceratinae.

- an *Epicheloniceras* level (beds M6-M81 at La Marcouline). At the base of this interval *Cheloniceras* is no longer present and *Epicheloniceras* appears. The species *Epicheloniceras martini* (d'ORBIGNY, 1841); *E. martinioides* CASEY, 1961; *E. debile* CASEY, 1961; *E. subnodosocostatum* (SINZOW, 1906); *E. eotypicum* CASEY, 1961; *E. gracile* CASEY, 1961; *E. buxtorfi* (JACOB & TOBLER, 1906); *E. waageni* (ANTHULA, 1899) and *E. tschernyschewi* (SINZOW, 1906) were collected here (Fig. 5).

2.B. Contribution of Douvilleiceratidae to Aptian biozonation

In addition to this informal subdivision based on successive generic faunal assemblages, the distribution of Douvilleiceratidae at Cassis (Figs. 2-5) made it possible to establish several zones and subzones (Fig. 6):

- late Bedoulian:
  - Hambrovi Subzone* (middle part of the Deshayesi Zone) (beds 148-160),
  - Meyendorffi Subzone (upper part of the Furcata Zone) (from bed 174 to at least as far as bed 178),
- early-middle Gargasian
  - Martini Zone (at least from bed M 6 to bed M 63), wîth three subzones, successively:
    - Debile (at least from bed M6),
    - Gracile (from bed M30),
    - Buxtorfi (from bed M51)

* The upper Bedoulian position of this subzone has recently been questioned by MORENO *et alii* (2007). We discuss this point in another paper (ROPOLO *et alii*, 2008).

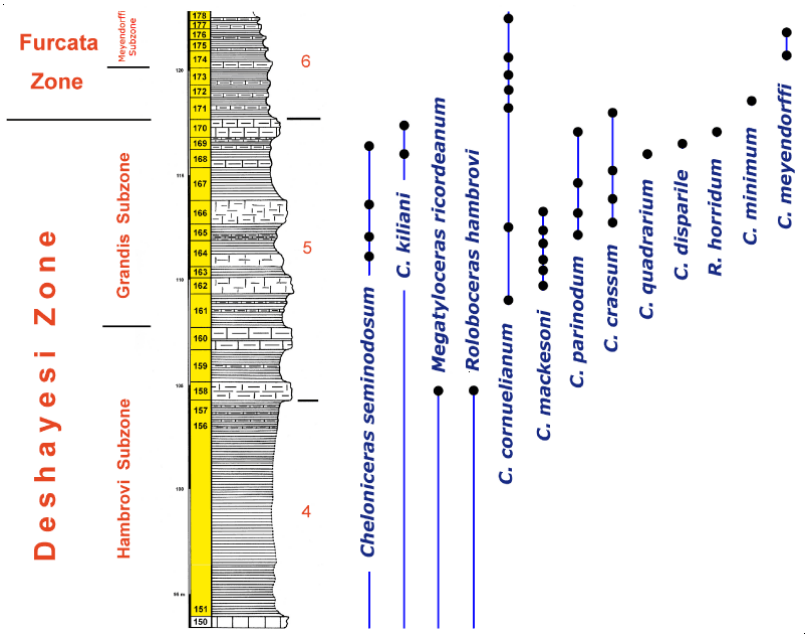


Figure 4: Lower Aptian (*pro parte*) composite section of the Cassis-La Bédoule area with the stratigraphic position of the collected Cheloniceratinae and Roloboceratinae.

The Melchioris Zone (from bed M 64 to at least bed M 81) is defined at La Marcouline by an association of several species belonging to the faunal group that commonly occurs with the index species. It was found in similar levels which crop out laterally a few km East of Roquefort-La Bédoule (to be published).

2.C. The Bedoulian-Gargasian boundary in the Lower Aptian stratotype

The lack of outcrops spanning the short interval between the top of the Comte quarry and the base of the la Marcouline quarry makes it impossible to be precise concerning continuity of the beds that include the Bedoulian/ Gargasian transition (CONTE, 1994; MOULLADE *et alii*, 2004). The only sector of the Cassis-La Bédoule area where this transition could be studied, the Les Tocchis section at La Bédoule (MOULLADE *et alii*, 2000, 2004, 2005) was made inaccessible in the late sixties as a result of urbanization. Micropaleontological samples were taken there in 1962 by one of us (M.M.), but macrofossils were never collected. The correlation between the uppermost levels of the Comte quarry, the middle part of Les Tocchis and the lowermost levels of La Marcouline is based only on microfaunal data (MOULLADE *et alii*, 2005; ROPOLO *et alii*, 2006). Thus, the levels of the last occurrences of *Dufrenoyia furcata* and *Cheloniceras meyendorffi*, as well as that of first occurrence of *Epicheloniceras* cannot be fixed, and consequently in the Lower Aptian stratotype the location of the Bedoulian-Gargasian boundary cannot be determined precisely. In this respect, recently studied sections at La Tuilière near Apt (DUTOUR, 2005; MOULLADE *et alii*, 2008) or in the Vocontian Basin (DAUPHIN, 2002) constitute more favorable localities in which to make this determination.

3. Systematic descriptions

In the following tables we will use the standard abbreviations generally accepted for the main shell parameters (Fig. 7):

D = maximum diameter
d = minimum diameter
Wh = whorl height
Uw = umbilical width
Wb = whorl breadth
(The ratio Wb/Wh expresses the degree of compression of the shell)
K = number of ribs per half whorl
Ph = diameter at the end of phragmocone
(E) evolute morphotype
(S/E) semi-evolute morphotype
(I) involute morphotype
All measurements in mm.

Material: Specimens from the ROPOLO collection are designated by numbers preceded by the mentions PRB for the Barremian, PRA for the Lower Aptian, PRAG for the middle Aptian (Gargasian). CONTE's collection is labeled "C" for the Lower Aptian, and C.G. for the middle Aptian. The material from the Museum of Paleontology, University of Provence, Campus Saint-Charles (Marseilles) is labeled "Sc". A few specimens described here are from the DEROGNAT Collection. All collections are deposited in the University of Provence Museum.

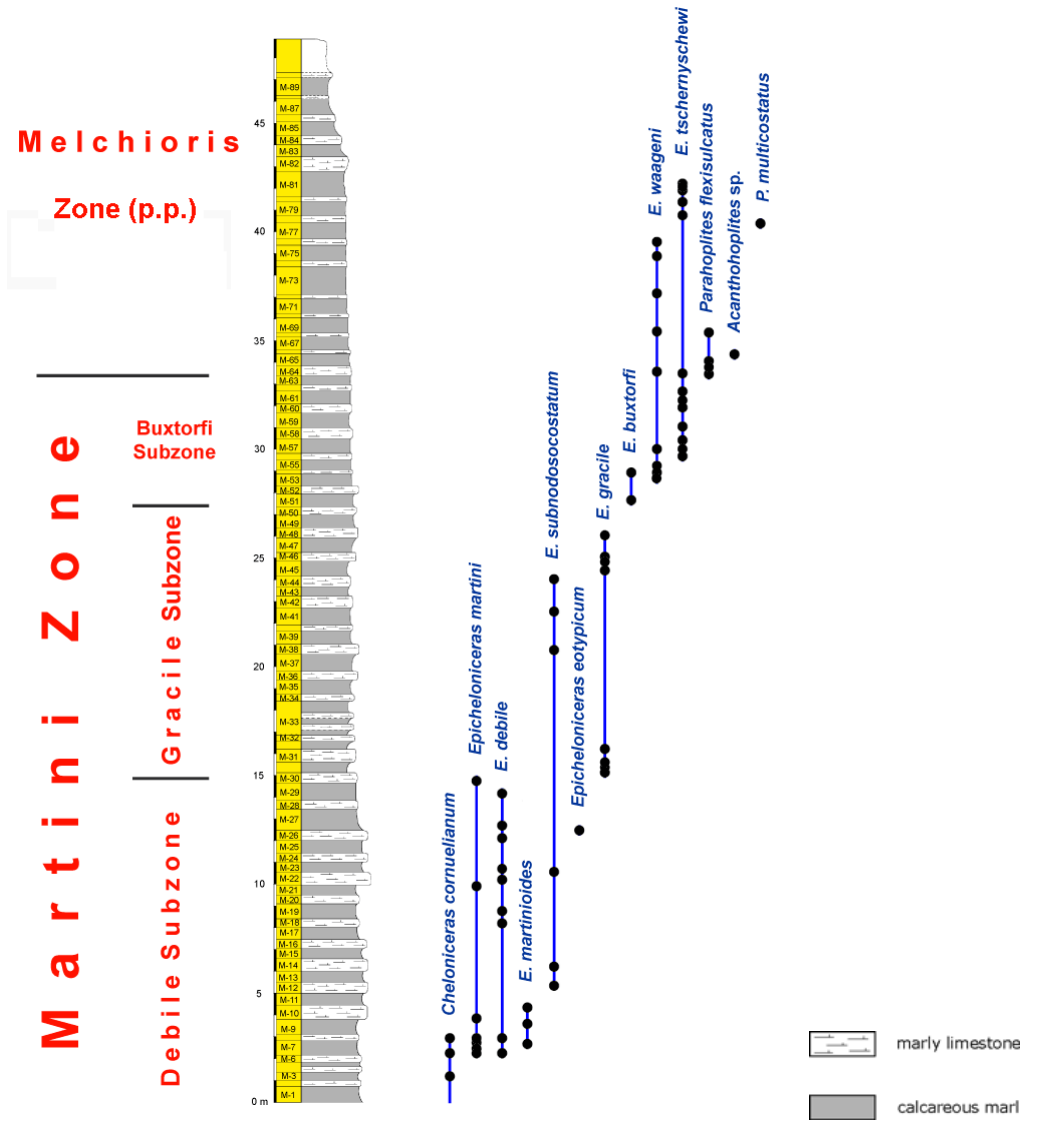


Figure 5: Middle Aptian in the La Marcouline Quarry section, with the stratigraphic position of the collected Cheloniceratinae.

Family Douvilleiceratidae
PARONA & BONARELLI, 1897

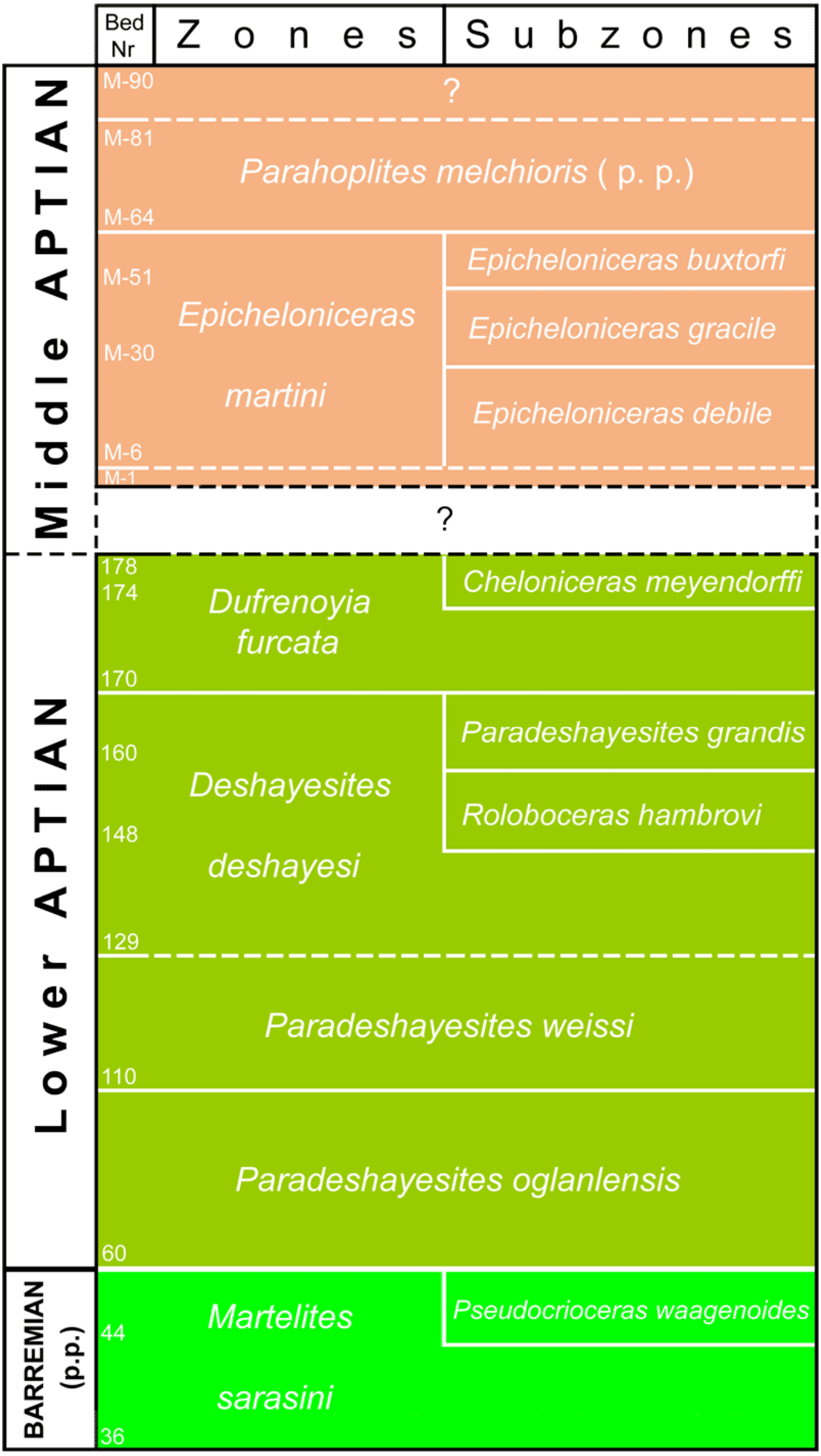
Subfamily Cheloniceratinae
SPATH, 1923

Genus *Prochelonicerasl*
SPATH, 1923

Type-species: *Ammonites stobieskii* d'ORBIGNY, 1850a (p. 113, Lower Aptian of southeastern France).

Diagnosis: Ammonite slightly involute, generally of great size, with wide umbilicus, rounded whorls of medium thickness. Whorl section is wider than high. Ribs are strong, radial, or slightly inclined backward. They bear umbilical and lateral tubercles, the umbilicals being stronger than the lateral ones. Ribs are generally simple but some of them may bifurcate from the umbilical tubercle. Short secondary ribs are sometimes present on the young whorls, but the number of intermediate ribs is low.

▶ **Figure 6:** Latest Barremian to middle Aptian biozonation in the stratotypical area of Cassis-La Bédoule, SE France. Upper Barremian / Lower Aptian bed numbering is that used in MOULLADE *et alii* (2000); middle Aptian bed numbering is specifically used in this paper for the La Marcouline Quarry section.


Bed Nr
Z o n e s
S u b z o n e s
Middle APTIAN
Lower APTIAN
BARREMIAN (p.p.)
M-90
?
M-81
Parahoplites melchioris (p. p.)
M-64
M-51
Epicheloniceras martini
M-30
M-6
M-1
Epicheloniceras buxtorfi
Epicheloniceras gracile
Epicheloniceras debile
?
178
174
Dufrenoyia furcata
170
Cheloniceras meyendorffi
160
Deshayesites deshayesi
148
129
Paradeshayesites grandis
Roloboceras hambrovi
Paradeshayesites weissi
110
Paradeshayesites oglanlensis
60
44
Martelites sarasini
36
Pseudocrioceras waagenoides

Prochelonicera pachystephanum (Uhlig, 1883)

(Pl. 1, figs. 1-3)

1883 *Acanthoceras Pachystephanus* Uhlig 1883, p. 255, Pl. 24, figs. 1.a-b & 2; Pl. 25, fig. 1.

1906 *Douvilleiceras pachystephanum* (Uhlig 1883); Sinzow, p. 169, Pl. 4, figs. 3.a-b.

1915 *Douvilleiceras pachystephanum* (Uhlig 1883); Kilian & Reboul, p. 61, Pl. 3 fig. 4; Pl. 4, fig. 8; Pl. 8, figs. 1 & 4.

1933 *Douvilleiceras pachystephanum* (Uhlig 1883); Rouchadze, p. 187.

1960 *Prochelonicera pachystephanum* Uhlig; Kudriavtsev, p. 336, Pl. 17, fig. 1; Pl. 19, figs. 1-2.

1994 *Prochelonicera* gr. *pachystephanum/albrechtiaustriae* Delanoy, Pl. 6, fig. 4.

1997 *Prochelonicera* gr. *pachystephanum/albrechtiaustriae* Delanoy, Pl. 24, fig. 7.

1997 *Prochelonicera pachystephanum* (Uhlig); Aguado et alii, Pl. 7, fig. a.

1999 ? *Prochelonicera pachystephanum* (Uhlig 1883); Ropolo *et alii*, Pl. 7, fig. 3.

2004 *Prochelonicera* sp. A, Sharikadze *et alii*, p. 316-317, Pls. 5-6; p. 432-433.

2005 *Prochelonicera pachystephanum* (Uhlig); Kotetishvili *et alii*, p. 379, Pl. 91, figs. 1.a-b.

Material: Three complete specimens: PRB 0419, PRA1320, PRA1322, several fragments.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRB0419	70	27	28	25.65	18	60	0.95	E
PRA1320	102	40	38	38.4	18	-	0.96	E
PRA1322	159	49.8	53.5	49.3	18	122	0.98	E

Description: Evolute coronatiform ammonite, with wide oval whorl section, rounded venter and depressed wide umbilicus. Ribs are strong, radial, more often simple. Rare intermediate ribs are irregularly intercalated between main ribs. They can start from the umbical wall or from mid flank. All ribs pass straight over the venter. On the flanks, primaries bear strong umbilical and lateral tubercles, the umbilicals stronger than the laterals. Intermediate ribs, thinner, are non-tuberculate.

Discussion: Our specimens are sligthtly compressed, but are very similar to the forms illustrated by Uhlig (1883: Pl. 24, figs. 1.a-b & 2), with 18 strong ribs per half whorl. They differ from the form of Pl. 25, fig. 1, which shows a more prominent ornamentation and only 14 ribs per half whorl.

Occurrence: The vertical range of *Prochelonicera pachystephanum* seems to be very long. We collected this species from the Late Barremian *Pseudocrioceras waagenoides* Zone (Le Brigadan section), the Early Aptian *Paradeshayesites oglanlensis* (Les Caniers section) and *Paradeshayesites weissi* (Les Fourniers section) zones.

Prochelonicera albrechtiaustriae (Hohenegger, *in* Uhlig, 1883)

(Pl. 2, figs. 2-3; Pl. 3, figs. 1-2; Pl. 4, fig. 2)

1883 *Acanthoceras Albrechti-Austriae* Hohenegger *in coll.* Uhlig, p. 129, Pl. 22; Pl. 23, fig. 1.

non 1902 *Acanthoceras Albrechti-Austriae* Hohenegger; Koenen, p. 140, Pl. 41, fig. 1.

1906 *Douvilleiceras Albrechti-Austriae* (Hohenegger); Sinzow, p. 167, Pl. 4, figs. 1-2.

1915 *Douvilleiceras Albrechti-Austriae* (Hohenegger) Uhlig; Kilian & Reboul, p. 57, Pl. 1, fig. 6; non Pl. 3, fig. 5; Pl. 8, fig. 3.

1927 *Douvilleiceras Albrechti-Austriae* (Hohenegger) Uhlig; Roch, p. 20.

1933 *Douvilleiceras Albrechti-Austriae* (Hohenegger); Rouchadze, p. 185, fig. 8

1958 *Prochelonicera albrechtiaustriae* (Hohenegger) (Uhlig); Luppov, Pl. 65, fig. 1.

1960 *Prochelonicera albrechtiaustriae* (Hohenegger); Kudriavtsev, p. 335, Pl. 16, fig. 1.

1967 *Prochelonicera albrechtiaustriae* (Hohenegger *in* Uhlig); Dimitrova, p. 175, Pl. 81, fig. 4; Pl. 85, fig. 5.

1972 *Prochelonicera albrechtiaustriae* (Hohenegger *in* Uhlig); Vasicek, p. 67, Pl. 10, fig. 6; Pl. 11, fig. 2.

1995 *Prochelonicera albrechtiaustriae* (Uhlig); Delanoy, Pl. 7, fig. 1.

1997 *Prochelonicera albrechtiaustriae* (Uhlig); Vasicek, Pl. 2, fig. 7.

2004 *Prochelonicera albrechtiaustriae* (Hohenegger *in* Uhlig); Sharikadze *et alii*, p. 314-315, Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, fig. 1; Pl. 4, fig. 1.

2005 *Prochelonicera albrechtiaustriae* (Hohenegger); Kotetishvili *et alii*, p. 380, Pl. 92, figs. 1.a-b & 2.a-b.

Material: Five complete specimens: Sc Dw403, Sc Dw302, Sc Dw12896, PRA1412, PRA1414 and numerous fragments and incomplete specimens.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
Sc Dw403	165	60	48.2	52	22	120	0.86	E
Sc Dw302	163	68	47	51.8	22	-	0.76	E
Sc Dw12896	156	56.5	45	53 (d=130)	22	-	0.93	E
PRA1412	148	59	40	51	20	-	0.864	E
PRA1414	92	29.5	22	25	19	-	0.84	E

Description: Evolute ammonite generally of large size with rounded inflated whorls. Section in the juvenile is wider than high, then, in the adult, it becomes higher than wide. Ornamentation of flanks consists of strong simple radial ribs bearing lateral and umbilical tubercles and of non-tuberculate intermediate ribs. Primaries start from the umbilical tubercle. Intercalatories originate generally from mid flank or from the first third of the flank. Between tubercles, main ribs are flattened. Then they rapidly become stronger. All the ribs pass straight over the ventral part. In this species, specific variability can be very important. Ribs are radial or slightly inclined backward, equal or variable in breadth, robust or rather weak. In the gerontic stage the ribs become more widely separated, intercalatories become as robust as the primaries and tubercles disappear. The umbilicus ranges in size from moderately to very wide. The number of ribs per half whorl varies from 14 to 24 according to diameter.

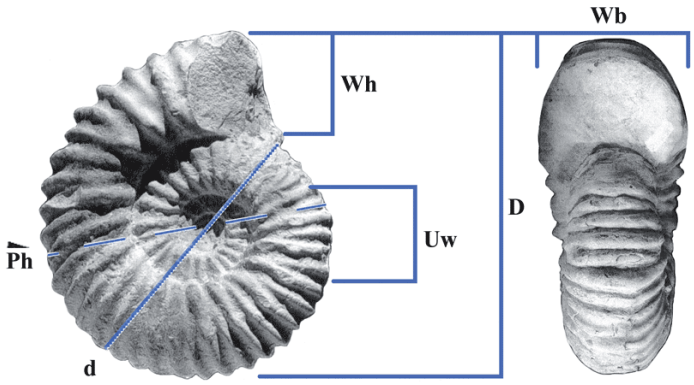


Figure 7: *Douvilleiceras Albrechti-Austriae* (HOHENEGGER) UHLIG: *in* KILIAN & REBOUL, p. 57, Pl. 1, fig. 6, topotype (Institut DOLOMIEU Collection, Grenoble, France).

Discussion: Our material is similar to UHLIG's (1883) original illustrations (Pl. 22 & Pl. 23, fig. 1) in the general shape of the shell and in the sculpture. But the figure on Pl. 22 has more ribs (24) per half whorl and is probably a gerontic specimen. Our specimen labeled PRA1413 (Pl. 2, fig. 2) resembles more exactly UHLIG's Pl. 23, fig. 1. The specimen illustrated by KILIAN & REBOUL (1915: Pl. 1, fig. 6) differs in having more intermediate ribs which occur irregularly between the main ribs. KILIAN & REBOUL's (1915: Pl. 3, fig. 5 and Pl. 8, fig. 3) listed under the name *Prochelonicera albrechtiaustriae* are probably *Chelonicera*.

Occurrence: *Prochelonicera albrechti-austriae* is well represented in paleontological collections, because it is the most common species of *Prochelonicera* collected in the Lower Aptian. Distribution: France (SE France, Drôme, Vocontian Basin, Vaucluse), Germany, Austria, Bulgaria, Poland, Romania, Czechia, North Caucasus, Russia, Georgia, Armenia, Mangyshlak (Kazakhstan), Mangyshlak (Iran), Colombia. At La Bédoule this species occurs throughout the lower part of the Lower Aptian *Paradeshayesites weissi* Zone (Les Fourniers section).

Prochelonicera stobieskii (d'ORBIGNY, 1850)

(Pl. 2, fig. 1; Pl. 5, figs. 1-4)

1850a *Ammonites Stobieckii* [sic] d'ORBIGNY, p. 113.

1889 *Ammonites Stobieskii* d'ORBIGNY; KILIAN, p. 248.

1895 *Ammonites Stobiesckii* [sic] d'ORBIGNY; KILIAN, p. 752, infrap. note n° 3.

1915 *Douvilleiceras Albrechti-Austriae* HOH. sp. var. *Stobiesckii* [sic] d'ORBIGNY; KILIAN & REBOUL, p. 51 & 58-61.

1927 *Douvilleiceras Albrechti-Austriae* HOH. sp. var. *Stobieskii* d'ORB.; ROCH, p. 20, Pl. 2.

1934 *Prochelonicera albrechti-austriae* var. *Stobieskii* d'ORB.; DENIZOT, p. 158.

1938 *Prochelonicera albrechti-austriae* var. *Stobieskii* d'ORB.; ROMAN, p. 425-426.

1981 *Prochelonicera stobieskii* (d'ORB.); CONTE, p. 65-70; p. 68, fig. 1.

Material: Three complete specimens Sc Dw301, PRA1417, PRA1420 and five fragments of whorls: PRA1418, 1421, 1422, 1423, 1427.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
Sc Dw301	196	81.2	52	70	26	-	0.862	I
PRA1417	222	90	61.2	58	24	181	0.644	I
PRA1420	194	78	48.6	68	20	-	0.871	I

Discussion: D'ORBIGNY never figured the type of this species, but briefly described it in the "Prodrome" (1850, p. 113):

"Grosse espèce, voisine d'*Ammonites mantelli*, mais avec des pointes sur les grosses côtes près de l'ombilic et d'autres sur les côtés, en tout quatre rangées."

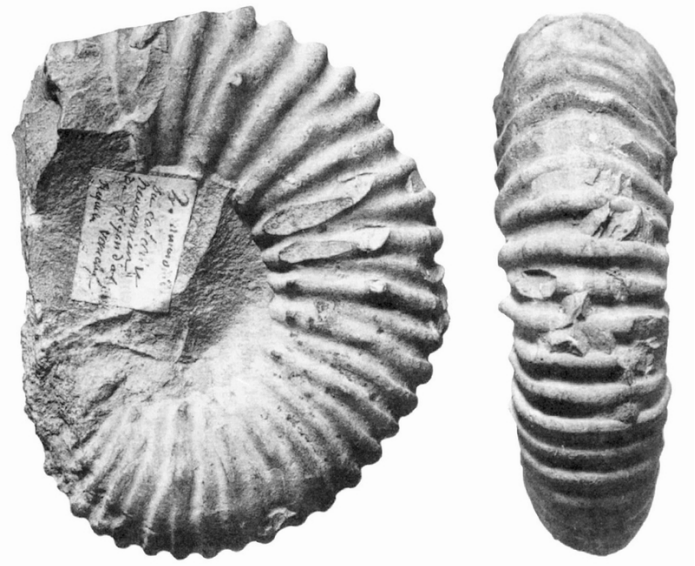


Figure 8: *Prochelonicera stobieskii* (d'ORBIGNY) specimen from the REQUIEN Collection, REQUIEN Museum – Avignon (France) (after CONTE, 1981 [Photograph BARTESAGO]).

KILIAN (1889, p. 248-249); KILIAN & REBOUL (1915, p. 59), without illustration or diagnosis, chose as the neotype of this species a specimen labeled by d'ORBIGNY himself (as "*Ammonites Stobieskii* - Ammonoïde du calcaire néocomien de Gigondas") which is included in the REQUIEN Collection deposited in the Avignon REQUIEN Museum (Fig. 8). Considering the similarities of this ammonite with the species figured by UHLIG, KILIAN & REBOUL named it "*Douvilleiceras Albrechti-Austriae*" var. "*Stobiesckii*" d'ORBIGNY.

The form figured by ROCH (1927, p. 20-21, Pl. II) is a marly calcareous internal mould which has lost practically all its lateral tubercles. Its umbilicus is very large and the sculpture consists of numerous strong radial main and intermediate ribs (26 per half whorl).

CONTE (1981) was the first to figure (text-fig. 10) and to give a complete description of the neotype (translation from the French):

Widely umbilicated form, whorls rather compressed, elevated whorl section, regular whorl growth, slightly involute. On the flanks, ornamentation consists of strong bituberculate ribs and non-tuberculate intercalatories branching at the umbilical tubercle or starting from the mid-flank.

Our material (Pl. 2, fig. 1 and Pl. 5, fig. 2) presents the same features as ROCH's specimen, with respectively 24 and 26 ribs per half whorl. Nevertheless, we also collected fragments of whorls that we attributed to the species "*Stobieskii*", because they resemble in both shell shape and sculpture the form figured by CONTE (REQUIEN Collection), although they have a coarser sculpture and a smaller number of ribs, with stronger tubercles (Pl. 5, fig. 1 & 4).

Occurrence: Lower Aptian, *Paradeshayesites weissi* Zone (Les Fourniers section).

Prochelonicera dechauxi (KILIAN & REBOUL, 1915)

(Pl. 4, figs. 1 & 3)

1915 *Douvilleiceras Martinii* var. *Dechauxi* KILIAN & REBOUL, p. 56, Pl. 1, figs. 7 & 7.b; Pl. 7, fig. 2.

2004 *Prochelonicera* aff. *dechauxi* (KILIAN & REBOUL, 1915); SHARIKADZE *et alii*, Pl. 7, fig. 1; Pl. 8, fig. 1.

Material: One complete specimen n° Sc Dw 302 and one fragment of whorl. PRA1422.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
Sc Dw302	145	48.2 (46:+ d=113)	38	24 (d= 113)	24	-	0.521	I

Description: Moderately involute coronatiform shell with flanks slightly convex and whorls which increase slowly in height. Wide umbilicus. Ornamentation consists of radial, irregular single ribs starting from the umbilical wall becoming stronger and spatulate on the upper part of the flank with thinner intermediate ribs originating at the first third of the side from a periumbilical tubercle. Main ribs bear two distant, strong, thorn-like tubercles. One is situated near the umbilical wall, the other near the ventro-lateral margin. In the adult, tubercles disappear.

Discussion: Our specimen is very similar to the shell represented by KILIAN & REBOUL (1915: Pl. VII, fig. 2), but has more ribs per half whorl. It differs from *Prochelonicera* aff. *dechauxi* figured by SHARIKADZE *et alii*, Pl. 7, fig. 1; Pl. 8, fig. 1, in having a wider umbilicus and a higher whorl section.

Occurrence: The complete specimen Sc Dw302 is in the DEROGNAT Collection, deposited in the Museum of Paleontology, University of Provence, Campus Saint-Charles, Marseilles. It is labeled only "La Bédoule" and its exact stratigraphic position is unknown. However, we collected from bed 116 (Lower Aptian, *Paradeshayesites weissi* Zone), in the Les Fourniers section, a fragment of whorl (n° PRA1422) that we can attribute without doubt to this species.

Genus *Cheloniceras* Hyatt 1903

Type-species: *Ammonites cornuelianus* d'Orbigny, 1841 (p. 364, Pl. 112, figs. 1-2, Lower Aptian).

Diagnosis: Coronatiform in the juvenile stage, but in the adult it has a suboctagonal to wide-oval whorl section, wider than high. Venter can be flat or slightly rounded. Ornamentation consists of strong radial single ribs bearing a pair of tubercles or in primaries dividing into two secondaries starting at mid flank from the lateral tubercle and forming a two branched fork. All ribs pass straight across venter or sometimes are slightly curved forward. The periumbilical tubercle smaller than the lateral one is directed downwards. The lateral tubercle forms a right angle with the axis of the shell. In some species (*Cheloniceras cornuelianum*, *Cheloniceras mackesoni*...), one or two narrower secondary ribs, starting from a round conical umbilical tubercle are intercalated between the main ribs. Occasionally a tertiary rib may be present. Umbilicus is wide (about one-third the diameter, a little more on gerontic specimens) with a high and steep border.

Almost all species that we collected at Cassis-La Bédoule are well described and illustrated by Casey (1961a, 1961b, 1962, 1980), Sharikadze *et alii* (2004) and Dutour (2005). Therefore we will describe our material only briefly, for it is of interest mainly in that it is now positioned precisely in the historical Lower Aptian stratotype succession.

Cheloniceras crassum Spath, 1930

(Pl. 6, figs. 1 & 3; Pl. 7, figs. 1-3)

1930 *Cheloniceras crassum* sp. nov. Spath, p. 449, Pl. 15, fig. 6.

1961b *Cheloniceras (Cheloniceras) crassum crassum* Spath; Casey, p. 208, Pl. 34, figs. 2-6; Pl. 35, fig. 4.

1967 *Cheloniceras (Cheloniceras) crassum crassum* Spath; Dimitrova, p. 171, Pl. 86, fig. 1.

2004 *Cheloniceras (Cheloniceras) crassum crassum* Spath; Sharikadze *et alii*, p. 328, Pls. 20-23; Pl. 24, fig. 1; Pl. 25.

Material: One measurable specimen; Sc Dw12609 (inner whorls are missing), numerous fragments of whorl (C.821, C.859, C.861...).

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
Sc Dw12609	181	62.2	~44	61	24	-	0.980	S/E

Description: Semi-evolute ammonite, with inflated flanks, rounded venter, depressed whorls, deep umbilicus. Whorl section is wide oval to suboctagonal. Ornamentation consists of radial ribbing, with alternating long and flat primaries starting from strong peri-umbilical tubercles and short weaker intermediate ribs which may be single or may unite to the main ribs in the lower part of the flank. In the adult stage the number of ribs is reduced, costation may be uniform, all ribs are more distant, becoming equal in thickness and prominence. Lateral tubercles are large and sharp but disappear with advanced age.

Discussion: The ornamentation of *Cheloniceras crassum* presents similarities with that of some adult *Cheloniceras cornuelianum* (d'Orbigny), showing the same type of radial ribbing. It is possible to collect all the transitional forms between the two species. Casey (1961b, p. 207, text-fig. 63) illustrated a specimen which shows characters of both *Ch. crassum* and *Ch. cornuelianum*. However, typical *Cheloniceras crassum* differ in having a small number of ribs which are stronger and more widely spaced, as well as thicker whorls and a wider umbilicus.

Occurrence: Lower Aptian, upper part of the *Deshayesites deshayesi* Zone, *Paradeshayesites grandis* Subzone and base of the *Dufrenoyia furcata* Zone (Comte Quarry section). This species has been found in the Lower Aptian of SE England, Georgia, Bulgaria and Colombia.

Cheloniceras kiliani (Koenen, 1902)

(Pl. 8, fig. 1)

1902 *Cheloniceras kiliani* sp. nov. Koenen, p. 406, Pl. 33, fig. 1.

1961b *Cheloniceras (Cheloniceras) kiliani* (Koenen); Casey, p. 213, text-fig. 67; Pl. 33, figs. 3-6.

1995 *Cheloniceras kiliani* (Koenen); Delanoy, p. 80, Pl. 4, fig. 2.

2004 *Cheloniceras kiliani kiliani* (Koenen); Sharikadze *et alii*, p. 324, Pl. 11, fig. 1; Pl. 12 fig. 1.

Material: Two complete specimens, PRA-1423, Sc Dw12900, numerous fragments.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1423	106	46	28	34	18	56	0.739	S/E
Sc Dw12900	158.2	52 (40, d=132)	60	34 (d= 132)	18	-	0.85	S/E

Description: Semi evolute ammonite with rounded venter, wide-oval to sub-octagonal whorl section. Umbilicus width, a quarter of the total diameter. Sculpture consists of alternating thick radial ribs springing from the umbilical wall and weaker inerm intercalary ribs starting from mid flank. Main ribs show strong tubercles on the umbilical margin and on the upper third of the flank. On the young whorls, they can form a two branched fork at the lateral tubercle. Rarely, intermediate ribs may bifurcate, the point of branching being on the upper third of the flank.

Discussion: Like *Cheloniceras crassum*, this species can be confused with *Cheloniceras cornuelianum*. But it differs in its more irregular and less prominent costation, less convex flanks and thinner whorls. Intermediate ribs are less numerous and umbilical tubercles stronger than in the d'ORBIGNY species.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone, Comte Quarry section.

Cheloniceras meyendorffi (d'ORBIGNY, 1845)

(Pl. 12, fig. 2; Pl. 14, fig. 1)

1845 *Ammonites meyendorfi* [sic] d'ORBIGNY, p. 428, Pl. 32, figs. 4-5.
1906 *Douvilleiceras meyendorffi* (d'ORBIGNY); SINZOW, p. 161-164, Pl. 1, figs. 7-10.
1909 *Douvilleiceras meyendorffi* (d'ORBIGNY); SINZOW, p. 4.
1910 *Douvilleiceras meyendorffi* (d'ORBIGNY); KILIAN,, p. 340 & 342
1915 *Douvilleiceras meyendorffi* (d'ORBIGNY); KILIAN & REBOUL, p. 50.
1961 *Cheloniceras meyendorffi* (d'ORBIGNY); ERISTAVI, Pl. 4, fig. 7.
1962 *Cheloniceras meyendorffi* (d'ORBIGNY); CASEY, p. 222-226, Pl. 36, fig. 4; Pl. 37, figs. 11.a-b; text-figs. 73.a-d & 74.
2004 *Cheloniceras meyendorffi* (d'ORBIGNY); SHARIKADZE *et alii*, Pl. 14, fig. 2; Pl. 16, fig. 4; Pl. 17, fig. 1; Pl. 18, fig. 1; Pl. 19, fig. 19.
2005 *Cheloniceras* gr. *meyendorffi/seminodosum*, DUTOUR, p. 156-159, Pl. 19, figs. 7-8.

Material: one incomplete crushed specimen: PRA1460, and two fragments of whorl: C.872.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1460	123.8	49.6	26	30	26	-	0.604	S/E
C.872	97	40	~24	27.2	26	-	0.68	S/E
C.875	49	26	~13	18	22	-	0.69	S/E

Description: Our material is very similar to a specimen illustrated by CASEY (1962, text-figure 74, p. 225). Semi-evolute shell with a large umbilicus, rounded venter tending to flatten. On the internal whorls each primary rib springs from a prominent periumbilical tubercle and supports at mid flank a strong lateral spine. Between the main ribs are intercalated two or three thinner inerm ribs. In the adult, the rib-density increases and their aspect changes. Main ribs become thicker and stronger. Lateral tubercles are scarcer and tend to disappear. From the last lateral tubercles primary ribs split into two unequal branches: the anterior branch is somewhat weaker than the posterior one. At the end of the phragmocone all ribs become equal and tend to spatulate on the upper part of the flank.

Discussion: To identify our material, we referred to SINZOW (1906: Pl. 1, figs. 7-10) and CASEY's illustrations (1962: Pl. 36, fig. 4; Pl. 37, figs. 11.a-b; text-figs. 73-74). *Cheloniceras meyendorffi* presents some affinities with *Cheloniceras cornuelianum*, which may also have secondary ribs originating from the lateral tubercle but it differs in a more important rib-density and a more distant tuberculation. The holotype, a fragment of shell figured by CASEY (1962, p. 224, text-figs. 73.c-d) was artistically interpreted by d'ORBIGNY, who restored with licence (1845, Pl. 32, figs. 4-5) the missing part of his specimen as was often done at that time.

On the basis of nuclei collected in the Gargasian marls of SE France, DUTOUR (2005) concluded that there were similarities in *Cheloniceras meyendorffi* and *Cheloniceras seminodosum* and united these two taxa in one group. However, there are fundamental differences in the form and the ornamentation of these two species. *Ch. meyendorffi* has an irregular alternation of strong primaries and thicker intermediate ribs, and tubercles on the main ribs are strong and prominent. *Ch. seminodosum* has a more regular sculpture, all ribs become equal in dimensions on the venter, the main ribs bear sharper tubercles, the umbilicus is wider and the ratio Wb/Wh differs notably between the two species. At Cassis-La Bédoule, their ranges are separate: we collected *Ch. seminodosum* in the Deshayesi Zone, beds 144 to169 and *Ch. meyendorffi* in the Furcata Zone, beds 174 – 176.

Occurrence: Lower Aptian, upper part of the *Dufrenoyia furcata* Zone, Comte quarry section.

Cheloniceras seminodosum (Sinzow, 1906)

(Pl. 10, figs. 1-4; Pl. 15, figs. 5-6)

1906 *Douvilleiceras seminodosum* sp. nov. Sinzow, p. 165, Pl. 1, figs. 3 & 6

1910 *Douvilleiceras seminodosum* Sinzow; Kilian, p. 340, Pl. 9, fig. 1.

1910 *Douvilleiceras* nov. sp. (aff. *seminodosum*); Kilian, p. 340, Pl. 9, fig. 2.

1915 *Douvilleiceras seminodosum* Sinzow; Nikchitch, p. 51, Pl. 1, figs. 9a-d; Pl. 2, figs. 1.a-b.

1933 *Douvilleiceras seminodosum* Sinzow; Rouchadze, p. 189, Pl. 3, fig. 1.

1960 *Cheloniceras seminodosum* (Sinzow); Kudriavtsev, p. 338, Pl. 16, figs. 3.a-b.

1964 *Cheloniceras seminodosum* (Sinzow); Kemper, p. 48, Pl. 6, figs. 1.a-b & 2.

1970 *Cheloniceras seminodosum* (Sinzow); Kotetishvili, p. 99, Pl. 19, fig. 4.

1971 *Cheloniceras seminodosum* (Sinzow); Kvantaliani, p. 105, Pl. 16, fig. 2; text-figs. 62-63.

2004 *Cheloniceras seminodosum* (Sinzow); Sharikadze *et alii*, p. 322, Pl. 1, fig. 2; Pl. 3, fig. 2.

2005 *Cheloniceras seminodosum* (Sinzow); Kotetishvili *et alii*, p. 381, Pl. 92, fig. 3a-b; Pl. 93, figs. 1-3.

non 2005 *Cheloniceras* gr. *meyendorffi/seminodosum* Dutour, p. 156-159, Pl. 19, figs. 7-8.

Material: PRA1450, 5 half whorls, PRA1451, 1452, C.868, C.869, C.882 and numerous fragments.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1450	77	32	~18	34	24	-	1.06	S/E
C.881	73	33	~23.5	31 (d=58)	24	-	~0.99	S/E
PRA1451	71	32	~19.2	35	24	-	1.09	S/E
PRA1452	~59	21	~16	18	21	-	~0.857	S/E
C.868	~59	25	~13	19	22	-	~0.760	S/E
C.869	~57	26	~12	13	20	-	~0.5	S/E
C.882	~40	24	~11	18	24	-	~0.75	S/E

Description: Semi-evolute ammonite with rounded whorls increasing rapidly in height and a wide umbilicus. Sculpture consists of 1) radial main ribs starting from the umbilical wall often bifurcating from a lateral tubercle in the upper part of the flank into two equal secondary ribs and 2) two or three intermediate ribs intercalated between two main ribs. All ribs on venter are of uniform relief, broadened and slightly flattened.

Discussion: Our specimen PRA1450 (Pl. 10, fig. 4) is very similar (same number of ribs by half whorl and same general features) to that of figure 4.d, Pl. 1 of Sinzow (1906). It differs only by a more regular costulation and a lesser number of bifurcating main ribs.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone, Comte Quarry section.

Cheloniceras parinodum Casey, 1961

(Pl. 9, figs. 1 & 3; Pl. 10, fig. 5)

1961a *Cheloniceras (Cheloniceras) parinodum* sp. nov. Casey, p. 594, Pl. 84, fig. 1; text-fig. 14.a.

1962 *Cheloniceras (Cheloniceras) parinodum* Casey; Casey, p. 219-222, text-figs. 70-72.

1980 *Cheloniceras (Cheloniceras) parinodum* Casey; Casey, p. 653, Pl. 110, fig. 1.

2004 *Cheloniceras (Cheloniceras) parinodum* Casey; Sharikadze *et alii*, p. 327, Pl. 26, fig. 1; Pl. 27, fig. 1.

Material: two flattened and broken specimens: C.s102, C.s103, some fragments of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
C.s102	150	59.8	35	~40	23	-	~0.668	S/E
C.s103	115	46	~26	32	22	-	~0.695	S/E

Description: Semi-evolute shell with wide oval to suboctagonal whorl section increasing moderately in height. Umbilicus is about a third of total diameter. Steep umbilical wall. Ornamentation consists of coarse radial primary ribs starting from a strong umbilical tubercle and bearing on the upper third of the flanks a lateral tubercle and intermediate ribs. Main ribs can be single or bifurcated, these form a two branched fork at the lateral tubercle, the anterior branch being stronger than the posterior one. Sometimes intercalary ribs appear at the first third of the flank or at mid-flank. On the venter, all ribs are of equal relief.

Discussion: The two incomplete shells that we describe are bituberculated, but we also collected some fragments which present on the main ribs, as on the holotype and a syntype illustrated by Casey (1962, p. 220, text-fig. 70; 1980, Pl. CX, fig. 1.a) a kind of elongated node or swelling uniting the umbilical tubercle with the lateral one; this character seems to be a

pecularity of some adult specimens. *Cheloniceras parinodum* presents similarities with *Cheloniceras cornuelianum*, but differs in a narrower and shallower umbilicus, a smaller number of ribs, and a coarser sculpture.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone (*Paradeshayesites grandis* Subzone) and lowermost part of the *Dufrenoyia furcata* Zone, Comte Quarry section.

Cheloniceras disparile CASEY, 1961

(Pl. 9, fig. 2)

1961b *Cheloniceras (Cheloniceras) disparile* sp. nov. CASEY, p. 215, Pl. 34, figs. 7.a-b & 8.a-c; text-figs. 67.g & 68.

2004 *Cheloniceras (Cheloniceras) disparile* CASEY; SHARIKADZE *et alii*, p. 319-320, Pl. 24, fig. 2.

Material: One specimen - PRA1452, Lower Aptian

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1452	53.8	25	13.5	15	24	-	0.6	S/E

Description: Small semi-evolute ammonite with rounded whorls increasing moderately in height, a deep umbilicus, an abrupt wall and robust costation. Sculpture consists of main ribs of various thicknesses, starting from the umbilical tubercle or from the umbilical wall and bifurcating at mid-flank from a lateral tubercle, the anterior branch being stronger than the posterior one. One or two thinner non tuberculate intermediary ribs, starting from mid-flank or from the umbilical border, are intercalated between the primary ribs.

Discussion: This rare species has similarities with *Cheloniceras cornuelianum* (d'ORBIGNY), from which it is transitional toward the genus *Epicheloniceras*. According to CASEY (1961b, p. 215), it has a similar suture-line. The poor preservation of our specimen made it impossible to verify this fact and for this reason, we maintain its original status. It differs from the species of d'ORBIGNY in having unequal ribs (the branches of bifurcation are of unequal strength), narrower and less depressed whorls.

Occurrence: We collected this form at the top of the *Deshayesites dehayesi* Zone (*Paradeshayesites grandis* Subzone) in the Comte quarry section.

Cheloniceras quadrarium CASEY, 1962

(Pl. 11, fig. 1.a-b)

1962 *Cheloniceras (Cheloniceras) quadrarium* sp. nov. CASEY, p. 227-229, Pl. 36, fig. 7; Pl. 37, fig. 10; text-figs. 76 & 77 a-f.

2004 *Cheloniceras (Cheloniceras) quadrarium quadrarium* CASEY; SHARIKADZE *et alii*, p. 332-333; Pl. 8, fig. 2; Pl. 9, fig. 1; Pl. 10, fig. 1.

Material: A poorly preserved half specimen: C.873

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
C.873	270	83	~62	~76	~24	-	~0.915	S/E

Description: Large and compressed semi-evolute specimen with very inflated whorls. On the external whorl costation consists of radial rounded main and intercalary ribs separated by narrow interspaces. On the young whorl robust main ribs are bituberculated, each rib bearing a strong umbilical tubercle and a lateral one. Some main ribs can divide into two narrow branches starting from the lateral tubercle. General pattern and inner whorl are similar to the form illustrated in CASEY (1962, p. 228, text-fig. 76).

Discussion: This species, rare in SE France, has narrower and less strongly developed tubercles than *Cheloniceras seminodosum* SINZOW, *Cheloniceras (Cheloniceras) disparile* CASEY, and *Cheloniceras cornuelianum* d'ORBIGNY. It differs also from these species in its very inflated whorls and wider umbilicus.

Occurrence: *Deshayesites deshayesi* Zone (upper part of the *Paradeshayesites grandis* Subzone), Comte quarry section.

Cheloniceras mackesoni CASEY, 1962

(Pl. 12, fig. 1; Pl. 13, fig. 1)

1962 *Cheloniceras (Cheloniceras) mackesoni* sp. nov. CASEY, p. 231-234, Pl. 36, figs. 1 & 2.a-b; text-figs. 78, 79.a & 80.

1968 *Cheloniceras* aff. *mackesoni* CASEY; KEMPER, p. 72, Taf. 25, fig. 4.

Material: Seven specimens: PRA1451, PRA1452, PRA1463, PRA1464, PRA1467, PRA1470, C.475 and five pieces of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1451	355.5	150	94	109	36	-	0.72	S/E
PRA1452	410	158	131	131	37	-	0.829	S/E
PRA1463	428	160	120	137.5	38	d=350	0. 859	S/E
PRA1464	350	148	90	108.8	36	-	0.735	S/E
PRA1467	210	80	58	65.60	36	-	0.820	S/E
PRA1470	170	54	47	44.49	34	d=97.5	0.823	S/E
C.475	150	52	~40	45	36	-	0.865	S/E

Description: Large semi-evolute shells (some specimens approach 400 mm in diameter), whorls increasing moderately in height, suboctagonal to rounded whorl section. Costation consists of primary rounded ribs connected to the umbilical tubercle and in one, two or three intercalary ribs, irregularly distributed, some starting at mid-flank, others tending to bunch and in general joining the main ribs at the umbilical border. Umbilical tubercle is prominent and can form a sort of bulla. Lateral tubercles are feeble (some traces at mid-flank) and are completely absent on adult whorls. Main ribs are particularly prominent on venter and pass straight on the other side.

Discussion: Our material was determined by CASEY (personal communication, 1997). It is very similar to the typical forms figured by this author (1962, Pl. 36, figs. 1 & 2.a-b; text-fig. 78). This species presents relatively compressed whorls and cannot be confused with another taxon. It differs from other Cheloniceras in its ribbing which resembles that of Parahoplites, with umbilical nodes on the inner whorls which become discrete tubercles on the adult and then tend toward absence on the last whorl.

Occurrence: *Deshayesites deshayesi* Zone (*Paradeshayesites grandis* Subzone), Comte quarry section.

Cheloniceras cornuelianum (d'ORBIGNY, 1841)

(Pl. 14, figs. 2.a-b; Pl. 15, figs. 1-3; Pl. 16, fig. 1)

1841 *Ammonites Cornuelianus* d'ORBIGNY, p. 364, Pl. 112, figs. 1-2.

1960 *Cheloniceras cornuelianum* ORBIGNY (?);KUDRIAVTSEV, p. 336-337, Pl. 18, figs. 1.a-b, 2.a-b & 3.

1961b *Cheloniceras (Cheloniceras) cornuelianum* (d'ORBIGNY); CASEY, p. 198, Pl. 33, fig. 7; Pl. 34, figs. 1 & 9; Pl. 35, figs. 1-3; text-figs. 60.a-c, 61-62 & 67.e-f

1979 *Cheloniceras cornueli* (d'ORB.); COLLIGNON *et alii*, p. 150.

2004 *Cheloniceras (Cheloniceras) cornuelianum* (d'ORBIGNY); SHARIKADZE *et alii*, p. 320-321; Pl. 11, fig. 2; Pl. 13; Pl. 14, fig. 1; Pl. 15, fig. 1.

2005 *Cheloniceras cornuelianum* (d'ORBIGNY); DUTOUR, p. 152-156, Pl. 19, figs. 1-6.

2005 *Cheloniceras cornuelianum* (d'ORBIGNY); KOTETISHVILI *et alii*, p. 381, Pl. 93, figs. 4.a-b.

Material: Seven specimens: PRA1456, C.876, C.874, PRA1457, PRA1458, C.877, C.878 (those four last specimens are pyritized nuclei) and numerous fragments of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1456	133.4	48	30	64	27	94	1.33	S/E
C.876	62.5	32	-	39.4	21	-	1.23	S/E
C.874	55	20	11.2	22	25	-	1.1	S/E
PRA1457	23	8.2	7	15	25	-	1.82	S/E
PRA1458	21	8.2	5.2	14	25	-	1.70	S/E
C.877	19	6.2	6	14.2	24	-	2.29	S/E
C.878	19	7	5	12.2	22	-	1.74	S/E

Description: Adult specimens are semi-evolute shells with rounded whorls increasing moderatly in height, but three stages of growth can be observed:

- an initial stage, or "*royerianum*" stage. As observed and figured by DUTOUR (2005: p. 154-155, Pl. 19, figs. 3.b & 3.e), and already hinted at but not convincingly demonstrated by NIKCHITCH (1915) and CASEY (1961b), the initial whorls of *Cheloniceras cornuelianum* are similar to the figuration of "*Ammonites royerianus*" d'ORBIGNY 1841 (Pl. 112, figs. 3-5). This stage is characterized by a very depressed subtrapezoidal section, flat whorls with strong lateral spinose tubercles and a deep crateriform umbilicus. Ornamentation consists of spaced ribs forming a twofold constriction. Between them the venter is smooth, without intercalary ribs. This morphologic stage can be also found in the young whorls of *Epicheloniceras martini*

(d'ORBIGNY) (DUTOUR, 2005, p. 155).

- an intermediary stage, showing, on a slightly rounded venter, the characteristic sculpture of *Cheloniceras cornuelianum*: main tuberculate ribs with two pairs of tubercles, followed by two smooth intercalary ribs.
- an adult stage: the section become rounded-subrectangular. The venter is now convex, the lateral tubercles are smaller and tend toward absence on the last whorl, the umbilical tubercles become stronger and more widely spaced. Main ribs bifurcate on the flanks, at different height; generally two branches originate from the lateral tubercle, but sometimes they can start from the umbilical one.

Discussion: We collected large specimens, generally in calcareous beds, that we considered macroconches, and small pyritized nuclei in marls. *Cheloniceras cornuelianum* seems to be a highly variable taxon. SHARIKADZE (2004) distinguished two groups in this species:

- one group with 38-48 thin ribs on one whorl, wide trapezoidal whorl section, flattened venter.
- a second group with a small number of thick ribs and a wide-oval whorl section with a rounded venter.

The problem is to know whether it is convenient to add a third, that would comprise the forms transitional to the genus *Epicheloniceras* (Fig. 9) which include the specimens similar in form and sculpture to *Cheloniceras cornuelianum*, but with incipient feeble ventral tubercles on the ventral part.

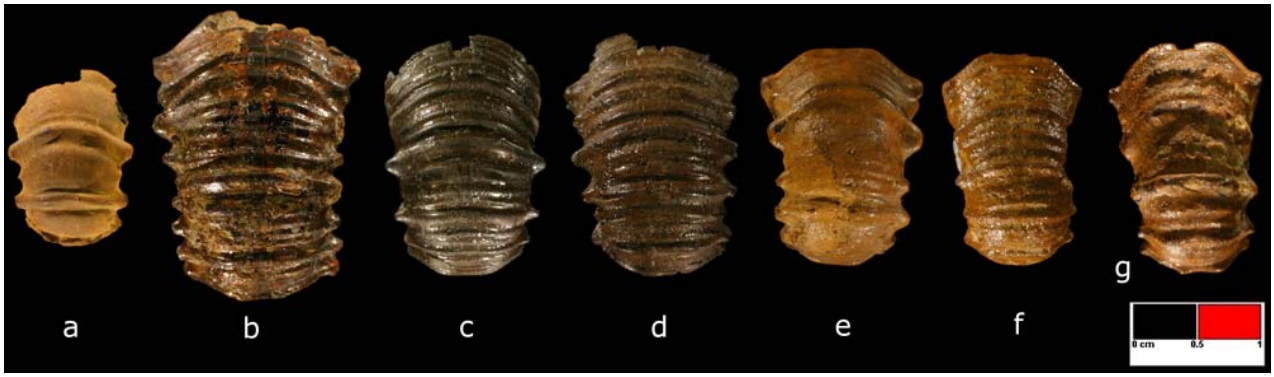


Figure 9: (from left to right): evolution of *Cheloniceras cornuelianum* towards *Epicheloniceras*. a) *Cheloniceras royerianum* (lowermost *Dufrenoyia furcata* Zone); b-d) *Cheloniceras cornuelianum* (*Dufrenoyia furcata* Zone); e-f) transitional forms to the genus "*Epicheloniceras*" and appearance of ventral tubercles = *Epicheloniceras martini* "ex-gr. *occidentalis*" (JACOB) (lowermost *Epicheloniceras martini* Zone); g) *Epicheloniceras martini martini* (d'ORBIGNY) = *Epicheloniceras martini* ex-gr. "*orientalis*" (JACOB) (*Epicheloniceras martini* Zone) [Photographs A. ARNOUX].

Occurrence: *Deshayesites deshayesi* Zone (*Paradeshayesites grandis* Subzone), *Dufrenoyia furcata* Zone, Comte Quarry section; *Epicheloniceras martini* Zone (base of the *Epicheloniceras debile* Subzone), La Marcouline section.

Cheloniceras minimum CASEY, 1962

(Pl. 15, fig. 4)

1961a *Cheloniceras* (*Cheloniceras*) sp. nov. CASEY, p. 609.

1962 *Cheloniceras (Cheloniceras) minimum* CASEY, p. 217, Pl. XXXV, figs. 5.a-c.

Material: one specimen: C.878

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
C.878	24.8	22	-	23	30	-	1.04	I

Description: Rare small shell, with wide venter, subquadrate whorls in section. On mid-flank small lateral tubercles. Ornamentation consists of primary ribs often bifurcating on the first third of flanks, and thin intercalaries which either extend to the umbilical border or disappear on flanks. Ribbing tends to become very uniform and sharp so primary ribs cannot be distinguished from secondaries.

Discussion: We collected *Cheloniceras minimum* at the base of the *Dufrenoyia furcata* Zone. The specimens of CASEY (1962) come from the *Deshayesites dehayesi* Zone, *Paradeshayesites grandis* Subzone.

Occurrence: extreme base of the *Dufrenoyia furcata* Zone, Comte quarry section.

Genus *Epicheloniceras* CASEY, 1954

Type species: *Douvilleiceras tschernyschewi* SINZOW (1906, p. 182, Pl. 2, fig. 11).

Diagnosis: Semi-evolute shell with very inflated whorls, wide umbilicus, oval whorl section. The venter is rounded, flattened, or broad, and can show thin intermediate ribs. Sometimes on the last whorl, all ribs are equal.

Three principal characters differentiate *Epicheloniceras* from *Cheloniceras*:

- the presence of three pairs of tubercles : ventro-lateral, lateral and umbilical,
- a mid-ventral depression on the ribs,
- main ribs bifurcating in two unequal or independent branches from the lateral tubercle.

These characters often disappear during ontogeny, and as a result adult or mature specimens may show a *Cheloniceras*-like morphologic pattern, particularly when they attain a large size; the ventro-lateral tubercles decrease progressively in prominence, shrink and finally disappear. Some *Epicheloniceras*, like *E. martini*, conserve a "*Cheloniceras royerianum*" stage in the initial whorls. From the strata transitional from the Furcata to the Martini Zone we collected all the forms transitional between *Cheloniceras* (morphotype *cornuelianum*) and the morphotype *Epicheloniceras* (*martini*) (Figs. 9-10).

However, *Epicheloniceras* is regarded as a discrete genus by many modern authors (CASEY *et alii*, 1998; SHARIKADZE *et alii*, 2004; DUTOUR, 2005), even though it is now well known that *Epicheloniceras* is an evolutionary stage derived by cladogenesis from an ancestral *Cheloniceras*. CASEY himself, in an early report once (1962, p. 235) proposed that *Epicheloniceras* be considered a subgenus, and confessed later (CASEY *et alii*, 1998, p. 532) that: "High in the following Walpen Clay and Sands (Meyendorffi Subzone) the *Cheloniceras* population contains a small minority of individuals with more advanced "*Epicheloniceras*" traits" (...).

On the basis of the pecularities of the sculpture in a rich pyritized material collected at La Tuilière near Gargas, DUTOUR (2005) clearly demonstrated the existence of an evolutionary trend between these two taxa. He separated two lineages that evolved during the deposition of the uppermost beds of the Lower Aptian (*Dufrenoyia furcata* Zone) and at the base of the middle Aptian (*Epicheloniceras martini* Zone) (p. 152):

- the lineage *Cheloniceras meyendorffi*/ *Cheloniceras seminodosum*, which leads to *Epicheloniceras eotypicum* in the overlying Martini Zone. This lineage is characterized mainly by the presence of a very isocostated stage starting with the first whorls;
- the lineage *Cheloniceras cornuelianum*/ *Cheloniceras crassum*, leading to *Epicheloniceras martini* with a commonly well developed "*royerianum*" stage, without ribbing between the very widely spaced main ribs or contrictions. This "*royerianum*" stage is clearly visible on his figures (op. cit., Pl. 19, figs. 3.b & d-e, for *Cheloniceras cornuelianum* and Pl. 25, figs. 1.b, d, f, h & 2.a-b & d-g for *Epicheloniceras martini*).

At Cassis-La Bédoule we too have followed, bed by bed, this progressive evolutionary process, for which we intend to discuss the possible taxonomic repercussions more thoroughly elsewhere. In this biostratigraphic paper, we will continue provisionally to consider *Epicheloniceras* a generic taxon.

Epicheloniceras martini (d'ORBIGNY, 1841)

1841 *Ammonites Martini* d'ORBIGNY, p. 194, Pl. 58, figs. 7-8, non fig. 9.

1905 *Douvilleiceras Martinii* d'ORBIGNY sp. var. *orientalis* JACOB, p. 412.

1960 *Epicheloniceras martini caucasica* KUDRIAVTSEV, p. 339, Pl. XX, figs. 2.a-b.

1960 *Epicheloniceras martini orientalis* (JACOB); KUDRIAVTSEV, p. 340, Pl. XXI, figs. 2.a-b.

1961a *Cheloniceras (Epicheloniceras) martinoides* CASEY, p. 595, Pl. 84, fig. 2; text-figs. 14.d-e.

1962 *Cheloniceras (Epicheloniceras) martinoides* CASEY; CASEY, p. 239, Pl. XXXVII, figs. 1.a-c & 2; Pl. XXXVIII, figs. 3.a-b; Pl. XXXIX, fig. 2; text-figs. 83 & 86.g-h.

1962 *Cheloniceras (Epicheloniceras) cantianum* CASEY, p. 242, Pl. XXXIX, figs. 10.a-b.

2005 *Epicheloniceras martini* (d'ORBIGNY); DUTOUR, p. 163-170, Pl. 20, figs. 1-4; Pl. 21, fig. 1; Pl. 22, figs. 1-2; Pl. 23, fig. 1; Pl. 24, figs. 1-6; Pl. 25, figs. 1-8 & 12.

2005 *Epicheloniceras martini* (d'ORBIGNY); KOTETISHVILI *et alii*, p. 384, figs. 2.a-b.

morphotype *martini* ex group "*occidentalis*" (JACOB, 1905)

(Figs. 10 & 11.c-d)

Material: 7 pyritic specimens: n° PRAG 1457, PRAG 1458, PRAG 1496, PRAG 1497, PRAG 1498, PRAG 1499, PRAG 1500, 5 calcareous shells: CG822, CG826, CG827, CG828, CG831 and numerous fragments of whorls.

Measurements: Pyritic specimens

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 1499	24.5	~10.5	8	15	23	-	1.42	S/E
PRAG 1457	21.2	7.6	7.8	18	22	-	2.36	S/E
PRAG 1458	20	8	6	14.9	22	-	1.86	S/E
PRAG 1496	15	7.9	5	12	22	-	1.51	S/E
PRAG 1497	12	6	3.6	9	19	-	1.5	S/E
PRAG 1498*	11	4.5	3.2	6.5	8	-	1.44	S/E
PRAG 1500	15	7.8	4.6	13	18	-	1.66	S/E

* *E. martini* morphotype "*occidentalis*", "*royerianum*" stage

Measurements: Calcareous specimens

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
CG832	~26	~12	-	18.2	20	-	~1.51	S/E
CG827	~24	10.2	-	~18	22	-	~1.76	S/E
CG822	~22.5	~7.9	-	18	22	-	~2.27	S/E
CG828	~22	~7.2	-	~14.2	18	-	~1.97	S/E
CG831	19	8	5.8	6 with d=17.5	19	-	~0.75	S/E

Description: Similar in form and ribbing to *Cheloniceras cornuelianum*, with a "*royerianum*" stage in initial whorls. Spaced ribs forming a twofold constriction ended by a strong and sharp lateral tubercle. One two or three non tuberculate intermediate ribs are intercalated between the main ribs. Then, on the primaries slightly depressed at mid-venter, appear two feeble ventro-lateral tubercles. The venter is flat or slightly convex, the umbilicus rather wide and deep.

Discussion: For the first time JACOB (1905, p. 412-413) distinguished two varieties of *Epicheloniceras martini* (d'ORBIGNY): *E. martini* var. "*occidentalis*" and *E. martini* var. "*orientalis*", each, according to the author, restricted to a discrete geographic area.

- The first variety is a form with a sub-hexagonal whorl section, a convex venter on which the primaries are bounded at each end by a conical spinose tubercle and which support two feeble ventro-lateral tubercles. This variety is characteristic of the "faciès occidental" (KILIAN, 1895, p. 762-765; JACOB, 1905) and occurs mainly at Gargas, Carniol and in the Apt region.
- The second variety has a stronger sculpture and a more rounded venter and is represented only by forms like those of figs. 7 and 8, Pl. 58 in d'Orbigny (1841); it can be collected in the "faciès oriental" (Kilian, 1895, 765-770), that is to say in the Vocontian Basin (Sisteron, Hyèges, Vergons, Barrême, Drôme region).

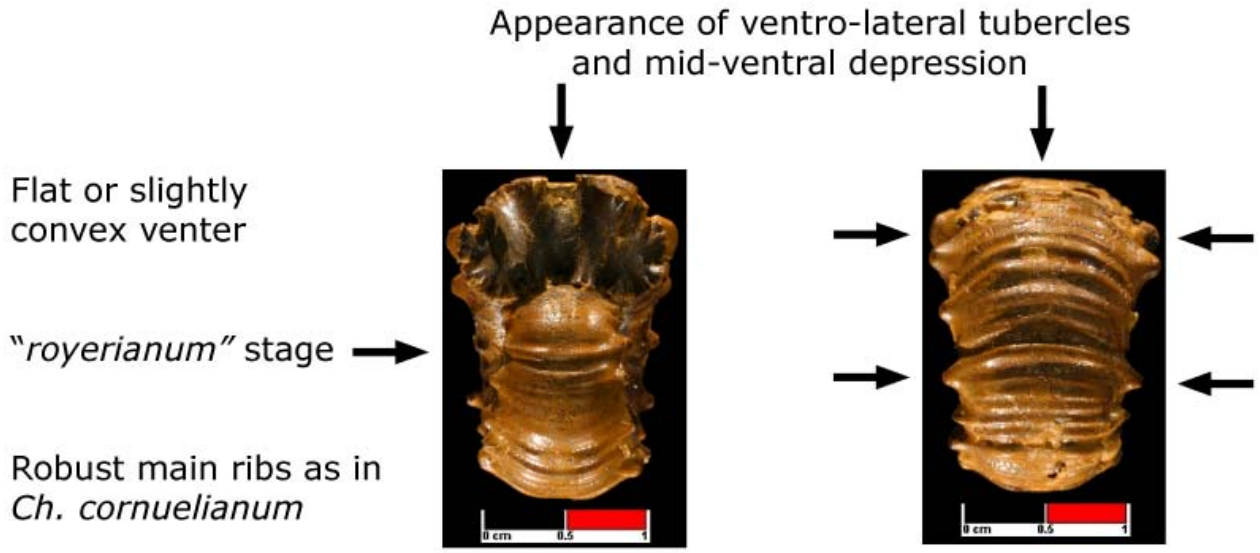


Figure 10: Characterization of several stages in a transitional form of *Epicheloniceras martini* [Photographs A. ARNOUX].

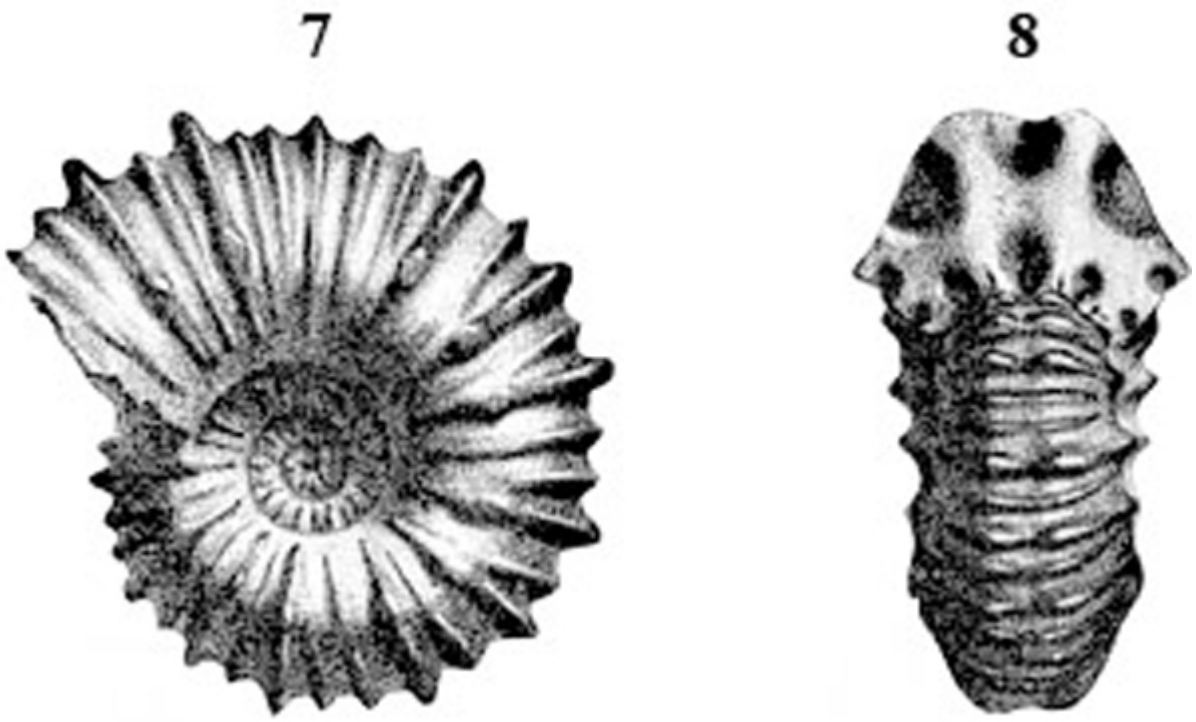


Figure 11: *Ammonites martinii* d'ORBIGNY in "Paléontologie française" (1841), Pl. 58, figs. 7-8.

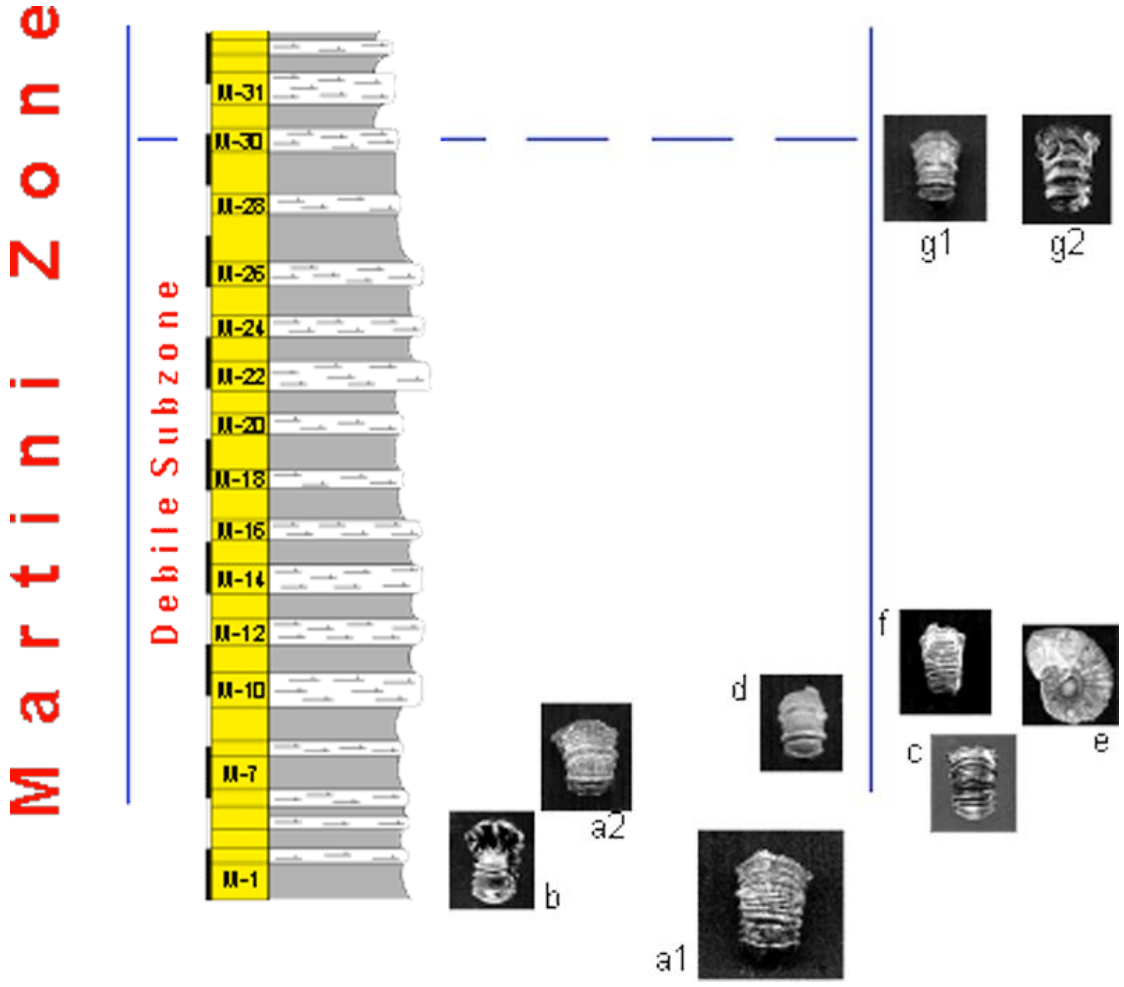


Figure 12: Scheme showing (at La Marcouline Quarry section, within the Debile Subzone) the progressive evolution from "*Cheloniceras cornuelianum*" to "*Epicheloniceras martini martini*". a1, a2) *Cheloniceras cornuelianum* – b) *Cheloniceras cornuelianum* "*royerianum*" stage - c) *Epicheloniceras martini* morphotype ex group "*occidentalis*" - d) *Epicheloniceras martini* "*royerianum*" stage - e) *Epicheloniceras martini* morphotype "*martinioides*" - f, g1, g2) *Epicheloniceras martini martini* (ex group "*orientalis*").

This proposal was based on an erroneous concept and led to numerous stratigraphic ambiguities and misinterpretations. In fact, these varieties are not synchronous and constitute successive steps in the evolution of *Epicheloniceras martini*. At Cassis-La Bédoule we collected *Epicheloniceras martini* morphotype "*occidentalis*" at the base of the *Epicheloniceras martini* Zone and the morphotype "*orientalis*" at the top of the *Epicheloniceras debile* Subzone.

Occurrence: *Epicheloniceras martini* Zone, *Epicheloniceras debile* Subzone (beds M-6 to M-10). La Marcouline Quarry section.

morphotype *martini* ex group "*orientalis*" sensu JACOB, 1905

(Figs. 11.f, 11.g1, 11.g2 & 12 - 13; Pl. 16, figs. 3-5)

Material: 3 pyritic specimens and numerous fragments; PRAG 1512, PRAG 1513, PRAG 1514; 3 calcareous specimens: CG829, CG 825, CG826 and numerous pieces of whorls

Measurements (Pyritic specimens):

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 1512	38.5	15.2	10	24	18	-	1.57	E
PRAG 1513	19	8.8	5	12	18	-	1.36	E
PRAG 1514	18	8.5	4.6	10	18	-	1.17	E

Measurements (Calcareous specimens):

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
CG829	28.5	11	8	18	20	-	1.63	E
CG825	26.2	9.2	6.8	12	18	-	1.30	E
CG826	16.5	~7	4	10	18	-	1.42	E

Description: Semi-evolute shell with very inflated whorls, wide umbilicus, about 40 per cent of total diameter, oval whorl section. The costulation consists of radial robust primaries and one, two or three thinner secondary ribs. Strong lateral and ventro-lateral tubercles.

Discussion: Differs from the morphotype "*occidentalis*" in having in immature whorls some similarities with *Epicheloniceras tschernyschewi* (SINZOW). It is difficult to separate microconchs of these forms.

Occurrence: *Epicheloniceras martini* Zone, *Epicheloniceras debile* Subzone (beds M-22 to M-30), La Marcouline Quarry section.

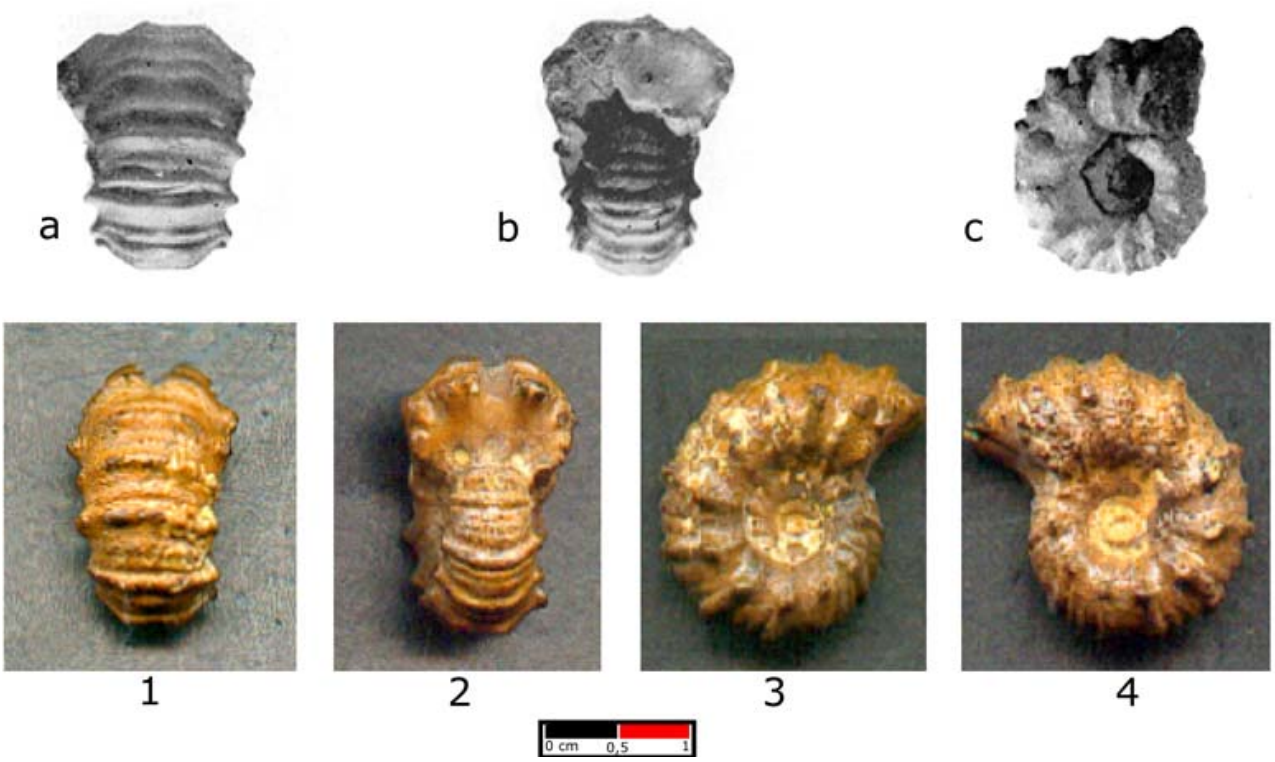


Figure 13: a-c: *Epicheloniceras martini* "*orientalis*" JACOB, *in* KUDRIAVTSEV 1960, Pl. XXI, figs. 2.a-c (venter still flat and wide as in *Cheloniceras cornuelianum*) – 1-4: *Epicheloniceras martini* (d'ORBIGNY), four views of the same specimen, La Marcouline Quarry section (venter rounded; this is the final stage of *E. martini*).

morphotype *martinioides* CASEY, 1961

(Fig. 11.e; Pl. 16, figs. 2 & 9)

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
CG911	65	26	15.5	24.8	26 (d=62)	d=50	0.95	S/E
CG912	48	20	16	29	23	d=38	1.45	S/E
CG913	39	15 (14, d=35)	9	21 (d=35)	24	d=27	1.4	S/E

Description: Similar in form and sculpture to *Epicheloniceras martini* but with stronger ventral and lateral tubercles and only one or two intermediate ribs. The young stage of this form (before D = about 40mm) can be confused with *Epicheloniceras tschernyschewi* (SINZOW). Mature specimens can be distinguished from the species of SINZOW by fewer secondary ribs and a more important whorl width.

Discussion: CASEY (1962, p. 241) did not find the types of *Epicheloniceras martini* in the collections of d'ORBIGNY in the Museum National d'Histoire Naturelle of Paris. As a result he erected a new species on the basis of specimens from the Lower Greensands of the Isle of Wight.

The group of *Epicheloniceras martini* shows a great variability. *Epicheloniceras martinioides* appears to be only a variety within this group, along with the conspecific "*orientalis*", "*occidentalis*", "*cantianum*" or "*alternatum*" morphotypes. In agreement with DUTOUR (2005, p. 164) we think that it is not necessary to separate the *martinioides* form as a species distinct from that of d'ORBIGNY.

Occurrence: Middle Aptian (Gargasian) *Epicheloniceras martini* Zone, Epicheloniceras debile Subzone (beds M-7 to M-10, La Marcouline Quarry section).

Material: 3 calcareous specimens: CG 911, CG912, CG913 and numerous fragments.

Epicheloniceras eotypicum CASEY, 1962

(Pl. 21, figs. 3 & 7-8)

1962 *Cheloniceras (Epicheloniceras) eotypicum* CASEY, p. 243, Pl. XXXVIII, figs. 4a-d; Pl. XXXIX, figs. 5a-b; text-fig. 86f.

2005 *Cheloniceras (Epicheloniceras) eotypicum* CASEY; DUTOUR, p. 182-184, Pl. 28, figs. 1-5.

Material: 3 specimens (PRAG 2017, PRAG 2018, PRAG 2015).

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 2017	60	25.5	13.5	20	20	-	0.78	E
PRAG 2018	37	16	12	11	18	-	0.68	E
PRAG 2015	31	13.8	8.8	15	20	-	1.08	E

Description: Evolute shell with a suboctagonal whorl section, rounded venter, wide umbilicus (about one third of the diameter). Sides are flat or gently convex. Ribbing consists of main ribs taking their origin from a vertical umbilical wall and of one or two intercalary ribs starting irregularly from the umbilical wall or from mid-flank. The primaries, often flattened on the flank, bear a feeble lateral tubercle at the first third of flank and from D=50 mm, a feeble ventro-lateral thorn-like spine. All the ribs run straight on the venter and show an adoral convexity.

Discussion: According to CASEY (1962, p. 244), juvenile specimens of *Epicheloniceras eotypicum* cannot be separated from the form "*Cheloniceras*" until they attain a relatively late stage of growth.

Occurrence: Middle Aptian (Gargasian) *Epicheloniceras martini* Zone, upper part of the *Epicheloniceras debile* Subzone, La Marcouline Quarry section.

Epicheloniceras debile CASEY, 1961

(Pl. 17, figs. 1.a-b & 2)

1961a *Cheloniceras (Epicheloniceras) debile* CASEY, p. 595, Pl. 84, figs. 3.a-b; text-fig. 14.b.

1962 *Cheloniceras (Epicheloniceras) debile* CASEY; CASEY, p. 244, Pl. XXXVII, figs. 3-7, text-figs. 85-86.b.

2004 *Epicheloniceras debile* CASEY; SHARIKADZE *et alii*, p. 357, Pl. 45, fig. 2.

2005 *Epicheloniceras debile* CASEY; DUTOUR, p. 175-177, Pl. 26, figs. 1-5; Pl. 27, figs. 6-9.

Material: 4 complete specimens: PRAG 1476, 1475, 1482, 1491 and 5 pieces of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 1482	134	57	36.9	43.2	20	d=114	0.75	E
PRAG 1476	63.2	23	15	17	18	-	0.73	E
PRAG 1475	21.6	8.5	5	12.5	22	-	1.47	S/E
PRAG 1491	15.6	5.8	4.8	9.7	22	-	1.67	S/E

Description: Evolute to semi-evolute shell with a wide-oval cross section in the young stage and a polygonal whorl section in the later stage. Venter is convex with a ventral sulcus between two rows of ventro-lateral tubercles, which as ontogeny progresses first become rounded nodes and then tend to disappear in the adult. Ornamentation consists of an irregular alternation of main ribs starting from sharp umbilical tubercles on the umbilical margin and of one to three thiner intermediate ribs. Main ribs bear at mid-flank radially elongated lateral tubercles. Interspace between primary and secondary ribs differs and each rib can be radial or slightly inclined forward.

Discussion: In spite of some similarities with *Epicheloniceras tschernyschewi* in the young, this taxon differs notably from the species of Sinzow (1906) in its irregular ribbing, thinner whorls, wider umbilicus, and the reduction of ventro-lateral tubercles. With growth, the flanks become higher and slightly flattened. *E. debile* differs from the *E. martini* morphotype *martinioides* in having more intermediate ribs, and more depressed and thinner whorls.

Occurrence: Middle Aptian (Gargasian) *Epicheloniceras martini* Zone, *Epicheloniceras debile* Subzone, La Marcouline Quarry section.

Epicheloniceras subnodosocostatum (Sinzow, 1906)

(Fig. 14; Pl. 18, fig. 1; Pl. 21, fig. 4)

1906 *Douvilleiceras subnodosocostatum* Sinzow, p. 175, Pl. II, figs. 1-8.

1915 *Douvilleiceras subnodoso-costatum* Sinzow; Nikchitch, p. 40-45 & p. 53, Pl. VI, figs. 4-7.

1960 *Epicheloniceras subnodoso-costatum* (Sinzow); Kudriavtsev, p. 342, Pl. XXII, figs. 4.a-b.

1962 *Cheloniceras (Epicheloniceras) sellindgense* var. *audax* Casey, p. 253, Pl. XXXVII, figs. 8.a-b; text-fig. 86.d.

1964 *Cheloniceras subnodosocostatum* (Sinzow); Kemper, p. 51, Pl. 8, figs. 1.a-b & 2.a-b.

1997 Cheloniceras subnodosocostatum (Sinzow); Immel et alii, p. 180, fig. 2.

non 2005 Epicheloniceras tschernyschewi [=Cheloniceras subnodosocostatum (Sinzow)]; Dutour, p. 170-173.

2005 *Epicheloniceras subnodosocostatum* (Sinzow); Kotetishvili *et alii*, p. 383, Pl. 93, figs. 6.a-b; Pl. 95, figs. 1.a-b.

Material: 12 complete specimens: PRAG 1477, PRAG 13915, PRAG 1478, PRAG 1479, PRAG 2130, PRAG 2131, PRAG 2132 CG4, CG6, CG7, CG8, CG9, and 7 half whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 1477*	54	26	15.6	17	15	-	0.65	S/E
PRAG 1479	52	24	13	18	16	-	0.75	S/E
PRAG 13915*	42	19.8	10	~17	12	-	0.85	S/E
PRAG 1478	39	16	9	18	15	-	1.12	S/E
CG 4	33	13.5	8	~17	15	-	1.25	S/E
PRAG 2130	30	11	7.8	13	15	-	1.18	S/E
CG7	30	12	~7.5	~12.8	15	-	1.06	S/E
CG6	29.9	12	~7.2	13	15	-	1.08	S/E
CG9	28.2	12	~7	~12.5	16	-	1.04	S/E
CG8	25.6	12.5	~7	~12	14	-	0.96	S/E
PRA2131	26	10	7.5	13.8	15	-	1.38	S/E
PRA2132	20	9.8	6	11	15	-	1.12	S/E

* Crushed specimens

Description: Evolute to semi-evolute shell with whorls strongly inflated, wide and octagonal whorl section. Ornamentation consists of strong trituberculate primary ribs and of one or two intermediate ribs between the main ribs. In the mature stage of growth the intermediate ribs may disappear. Thorn-like umbilical tubercles are situated at the umbilical margin. They can be radially elongated in the direction of the ribs in the adult. In the middle of the flanks are strong, sometimes flattened lateral tubercles which decrease as growth proceeds. External tubercles on the ventro-lateral area are prominent in early stages but then are more weakly salient.

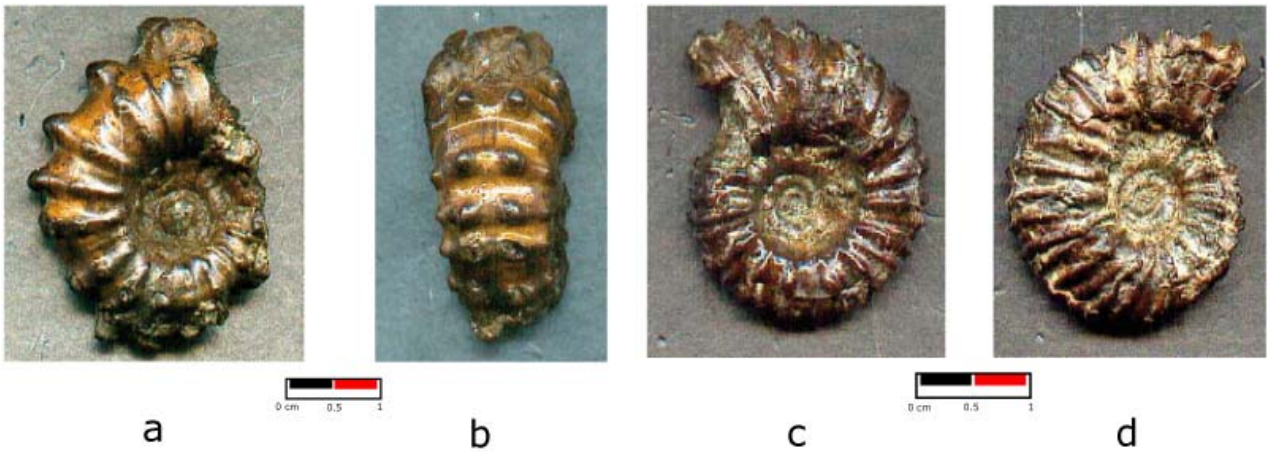


Figure 14: Typical pyritized specimens of *Epicheloniceras subnodosocostatum* (SINZOW, 1906), La Marcouline Quarry section - a-b) macroconch form, right side and ventral view; c, d) microconch form.

Discussion: *Epicheloniceras subnodosocostatum* differs in shape and sculpture from *Epicheloniceras tschernyschewi* (SINZOW) in having less numerous intermediary ribs, a whorl section which increase more rapidly in height and in more flattened flanks. In contrast with *E. martini* (d'ORBIGNY), *E. subnodosocostatum* is characterized by a greater inflation of the last whorl and an absence of sulcus on the ventral area between the ventro-lateral tubercles.

Occurrence: Middle Aptian (Gargasian); *Epicheloniceras martini* Zone, La Marcouline Quarry section.

Epicheloniceras gracile CASEY, 1961

(Pl. 19, figs. 1.a-b; Pl. 21, fig. 1)

1961a *Cheloniceras (Epicheloniceras) gracile* CASEY, p. 596, Pl. 81, figs. 1.a-b; text-fig. 14.c.

1962 *Cheloniceras (Epicheloniceras) gracile* CASEY; CASEY, p. 250, Pl. XXXVIII, figs. 2.a-b; Pl. XXXIX, figs. 1.a-b; text-fig. 86a.

2005 *Epicheloniceras gracile*, CASEY; DUTOUR, p. 178-180, Pl. 27, figs. 1-5.

Material: 5 specimens PRAG 1490, CG972, CG965, CG465, CG966, 1 incomplete specimen: labeled D10, DEROGNAT Collection, 1half whorl: CG914, numerous fragments of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
D10	157	67	35.2	36.4	36	-	0.54	S/E
PRAG 1490	154.2	62.3	37	44.6	28	d=118	0.71	S/E
CG914	~137	65	30	41.2	30	-	0.94	S/E
CG972	~98	43.5	~24	22	28	-	0.50	S/E
CG965	63	22.5	16.5	~17	30	-	0.75	S/E
CG465	30	17	9	~11	30	-	0.64	S/E
CG966	22	8.5	5	~6	25	-	0.70	S/E

Description: Semi-evolute ammonite with a coronatiform whorl section. From an early *tschernyschewi* stage on the nucleus, the shell evolves progressively to a martinioides stage, with umbilical, lateral and ventro-lateral tubercles and only one or two intermediate ribs between the main ribs. Then the costulation becomes denser with primaries irregularly distributed, being more prominent on the venter. In the adult, at very large diameters all ribs tend to be equal and flattened, some starting from the umbilical tubercle, other from the mid-flank. Lateral and ventro-lateral tubercles disappear. The venter is rounded, the umbilicus rather wide and deep.

Discussion: Our specimens differ from the lectotype in having a coarser and sharper sculpture, fewer and more distant ribs, and a wider umbilicus. They show close similarities with the variety "*rugatum*" CASEY, 1962, but they retain the three typical *tschernyschewi*, *martinioides* and *gracile* growth stages of the CASEY's species, and show no similarity with *Cheloniceras* aff. *meyendorffi* (KAZANSKY, 1914) as that English author has already pointed out.

Occurrence: Middle Aptian (Gargasian); *Epicheloniceras martini* Zone, *Epicheloniceras gracile* Subzone, La Marcouline Quarry section.

Epicheloniceras buxtorfi (JACOB & TOBLER, 1906)

(Pl. 18, fig. 2; Pl. 21, fig. 2)

1906 *Douvilleiceras Buxtorfi* JACOB & TOBLER, p. 15, Pl. I, figs. 9-11.

1915 *Douvilleiceras Buxtorfi* JACOB & TOBLER; NIKCHITCH, p. 45-47 & 53, Pl. VI, figs. 8-10.

1962 *Cheloniceras (Epicheloniceras) buxtorfi* (JACOB & TOBLER); CASEY, p. 253, Pl. XXXIX, figs. 8.a-b; text-figs. 88.l-p.

1964 *Cheloniceras buxtorfi* JACOB & TOBLER; KEMPER, p. 53, Pl. 11, fig. 1.

2004 *Epicheloniceras buxtorfi* (JACOB & TOBLER); SHARIKADZE *et alii*, p. 341, Pl. 34, fig. 2; Pl. 40, fig. 3.

2005 *Epicheloniceras buxtorfi* (JACOB & TOBLER); DUTOUR, p. 173-175, Pl. 28, figs. 7-10.

Material: 2 complete specimens PRAG 1510, PRAG 2011 and numerous fragments of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRAG 1510	61.5	28	15	~17	16	-	0.60	S/E
PRAG 2011	48.8	21.2	12.5	26	16	-	1.22	S/E

Description: Semi-evolute shell moderately increasing in height with a coronatiform wide-oval to subrectangular whorl section. Venter slightly convex becoming flat at the end of the first whorl. The sculpture consists of strong radial primary and one, rarely two, intermediary ribs. All ribs are separated by wide concave interspaces. On the ventral area, all ribs are feebly arcuate forward. From a lateral conical tubercle, main ribs can sometimes bifurcate at mid-flank into two unequal branches. Strong ventro-lateral tubercles. In the mature stage the costulation simplifies and resembles that of *Epicheloniceras subnodosocostatum*. On the body-chamber, ribs in uniform relief are unbranched.

Discussion: DUTOUR (2005) described and illustrated pyritized nuclei of *Epicheloniceras buxtorfi* and *E. subnodosocostatum*. Because of morphological similarities between the two species, the author considered them as conspecific. The first was thought to be the microconch, the second the macroconch of the same unique species, that is to say *Epicheloniceras buxtorfi*. This hypothesis is undoubtedly of great interest, but given the present state of our knowledge, great care must be taken to determine whether or not true dimorphism exists. To accept the dimorphism of taxa previously thought to be discrete, it is necessary to collect them in the same stratigraphic level, or even in the same bed. Unfortunatly, it seems that the range of *E. subnodosocostatum* differs from that of *E. buxtorfi*. At Cassis-La Bédoule we collected *E. subnodosocostatum* from beds 12 to 44 in the lower part of the Gargasian (*E. debile* and *gracile* subzones), and *E. buxtorfi* from beds 51 to 54, in a level just under the *Parahoplites melchioris* Zone and that stratigraphically is equivalent of the *E. buxtorfi* Subzone of CASEY (1961a).

Moreover there are morphologic dissimilarities between the two taxa. *E. buxtorfi* differs from *E. subnodosocostatum* in having a smaller number of intercalary ribs, a weaker sculpture and a different whorl section. For all these reasons we retain here an independent status for the two species.

Like *E. martini*, *E. buxtorfi* has an early "*royerianum*" stage, but this character disappears faster, at about d = 12mm. The cross-section becomes subrectangular, and the costulation may consist of 16 relatively widely spaced ribs as in the original material of JACOB & TOBLER (1906, Pl. I, figs. 9.a-b, 10.a-b, 11.b & d-e). *E. buxtorfi* differs from *E. tschernyschewi* in having a narrower umbilicus. Moreover, the species of SINZOW (1906) has higher and broader whorls and more numerous ribs.

Occurrence: Middle Aptian (Gargasian); *Epicheloniceras martini* Zone, *Epicheloniceras buxtorfi* Subzone, La Marcouline Quarry section.

Epicheloniceras waageni (ANTHULA, 1899)

(Pl. 22, figs. 1-3; Pl. 24, fig. 3)

1899 *Pachydiscus Waageni* ANTHULA, p. 106, Pl. 9, figs. 1.a-c.

1906 *Douvilleiceras meyendorffi* var. *waageni* (ANTHULA); SINZOW, p. 164, Pl. 1, fig. 10.

1913 *Douvilléiceras Meyendorffi* d'ORB. var. *Waageni* ANTH.; SINZOW, p. 109, Pl. VI, fig. 5.

1914 *Douvilleiceras waageni* (ANTHULA); KAZANSKY, p. 61, Pl. 3, figs. 37-38.

1960 *Epicheloniceras waageni* (ANTHULA); KUDRIAVTSEV, p. 342, Pl. 20, figs. 1-2; Pl. 21, fig. 1; Pl. 22, fig. 1.

1962 *Cheloniceras waageni* ANTH.; COLLIGNON, p. 40, Pl. CCXXXI, fig. 989.

1997 *Epicheloniceras waageni* (ANTHULA); IMMEL *et alii*, p. 182, Pl. 5, fig. 3.

2004 *Epicheloniceras waageni* (ANTHULA); SHARIKADZE *et alii*, p. 358-359, Pl. 49, fig. 1.

Material: 8 large specimens: CG921, CG951, D11, D10, CG922, CG920 CG948 and numerous fragments of whorls.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
CG921	325	134	~82	62	36	-	0.462	S/E
CG950	306	74	122.5 (116 d=280)	67 (d=280)	34	d=242	0.577 (d=280)	S/E
CG951	~246	108.5	~56	55	38	-	0.506	S/E
D11	220	97	-	45	38	-	0.463	S/E
D10	184	81	45.5	32	38	-	0.395	S/E
CG922	163	75.5	44	38	36	-	0.503	S/E
CG920	156	63	42.2	32	34	-	0.507	S/E
CG948	115.2	59	23	32	36	-	0.542	S/E

Description: Semi-evolute shell conforming with the specimen figured by ANTHULA (1899, p. 106, Pl. 9, figs. 1.a-c). Whorls strongly inflated, wide-oval cross section, rounded venter, flanks high and moderately convex, umbilicus moderately wide. Feeble elongated tubercles at mid-flanks. Ribbing consists of main ribs forking at the umbilical wall into two or three branches and in two or three simple intermediate ribs. All these ribs are slightly inclined backward on the flanks, except on the final whorl.

Remark: Our material is composed of large shells (D maximum = 325 mm), but they are often distorted, so the measurements of these fossil forms do not reflect the dimensions of the specimens before their burial.

Occurrence: Middle Aptian (Gargasian); *Epicheloniceras buxtorfi* Subzone, *Parahoplites melchioris* Zone, La Marcouline Quarry section.

Epicheloniceras tschernyschewi (SINZOW, 1906)

(Pl. 16, figs. 6-8 & 10; Pl. 18, fig. 3; Pl. 20, figs. 1.a-c; Pl. 21, figs. 5-6)

1906 *Douvilleiceras tschernyschewi* SINZOW, p. 182, Pl. II, figs. 11-12; Pl. III, figs. 2-8, non fig. 1.

1954 Cheloniceras (Epicheloniceras) tschernyschewi (SINZOW); CASEY, p. 113.

1962 *Cheloniceras (Epicheloniceras) tschernyschewi* (SINZOW); CASEY, p. 236, Pl. XXVIII, fig. 6; Pl.XXXIX, figs. 6-7; text-fig. 82.

1962 *Cheloniceras (Epicheloniceras) claudii* CASEY, p. 247, Pl. XXXVIII, fig. 5; Pl. XXXIX, figs. 4.a-b; text-figs. 86.e & 87.

1962 *Cheloniceras (Epicheloniceras) sellindgense* var. *audax* CASEY, p. 253, Pl. XXXVII, figs. 8.a-b; text-fig. 86.d.

1964 *Cheloniceras tschernyschewi* (SINZOW); KEMPER, p. 49, Pl. 11, fig. 5; Pl. 15, fig. 3.

1999 *Epicheloniceras* gr. *tschernyschewi* (SINZOW); CECCA *et alii*, Pl. 2, fig. 1; Pl. 3, fig. 1.

2004 *Epicheloniceras tschernyschewi* (SINZOW); SHARIKADZE *et alii*, p. 339, Pl. 32, fig. 2; Pl. 41, fig. 1; Pl. 42, fig. 1; Pl. 43, fig. 1; Pl. 44, fig. 1.

2005 *Epicheloniceras tschernyschewi* (SINZOW); DUTOUR, p. 170-173, Pl. 25, figs. 9-11.

Material: RG2010, CG970, CG971, PRAG 2000, PRAG 1998, PRAG 2012, PRAG 2014, and numerous fragments.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
RG2010	146	65.7	28	54.5	34	-	0.82	S/E
CG970	99	45	22.6	23	34	-	0.51	S/E
CG971	87	42	20	23	32	-	0.54	S/E
PRA2000	85	39	19	34	34	-	0.87	S/E
PRAG 1998	30	23.8	12	20	34	-	0.84	S/E
PRAG 2012	29	14.5	9	~13	18	-	0.89	S/E
PRAG 2014	29	14	8.8	~13	24	-	0.92	S/E

Description: Semi-evolute ammonite with strongly inflated whorls. Umbilicus about 35 per cent of the total diameter. The nucleus is indistinguishable from that of *Epicheloniceras martini*. On juvenile whorls the main ribs have three pairs of strong tubercles: umbilical, lateral and ventro-lateral. The umbilical tubercle is short and thorn-like; the lateral tubercle is situated in the middle of the flank and is radially elongated, but in later whorls it can develop into a sharp and high tubercle. From these tubercles the main ribs fork into two unequal branches, the anterior one being stronger than the posterior one. Between the main ribs there are one two or three thinner intercalary ribs. On adult shells the

tuberculation can disappear and all the ribs are denser, become equal and inclined backward on the flanks.

Discussion: This species shows a great variability. Some specimens have a less dense ribbing, a coarser sculpture and a wider umbilicus. Specimens collected in the La Marcouline Quarry section are similar to the topotype illustrated by CASEY (1962, text-fig. 82, fig. d).

Occurrence: Middle Aptian (Gargasian); *Epicheloniceras buxtorfi* Subzone, beds 56 - 62, *Parahoplites melchioris* Zone beds 64 – 81, La Marcouline Quarry section.

Subfamily Roloboceratinae CASEY, 1954

Genus *Roloboceras* CASEY, 1954

Type-species: *Ammonites hambrovi* FORBES 1845 (p. 354, Pl. 13, fig. 4)

Diagnosis: Semi-evolute shell, with deep and wide umbilicus, semi-circular or subtrapezoidal whorl-section, whorls inflated, increasing moderately in height, rounded venter at all stages of growth. High, flat umbilical wall. Sculpture consists of thick robust ribs passing over the venter and radially ornamented with lateral bullae or strong blunt tubercles. Some species may have robust main ribs with two, three or four intercalated secondary ribs, without tubercles, bifurcating at mid-flank or on the umbilical border. Tubercles can become very large (being almost comparable to those of *Megatyloceras*) in certain juvenile specimens such as those of *Roloboceras horridum* SPATH (Pl. 12, fig. 3).

Remark: Casey (1961b) suggested that in Great Britain the Roloboceratinae are "isolated stratigraphically from the Cheloniceratinae, though occurrences elsewhere in Europe show that the ranges of the two subfamilies overlap in the middle of the Lower Aptian" (p. 177). This is confirmed in the Cassis-La Bédoule area, in the Comte Quarry, where the Subfamily Roloboceratinae first occurs in bed 148 [*Roloboceras hambrovi* (Forbes)] and disappears in bed 170 [*Roloboceras horridum* Casey], whereas between these two beds, within the *Deshayesites deshayesi* Zone (precisely in the *Roloboceras hambrovi* and *Paradeshayesites grandis* subzones), we collected also *Cheloniceras kiliani*, *C. seminodosum*, *C. quadrarium*, *C. parinodum*, *C. disparile*, *C. crassum*, *C. mackesoni*, etc.

Roloboceras hambrovi (FORBES, 1845)

(Pl. 6, fig. 2)

1845 *Ammonites Hambrovii* FORBES, p. 354, Pl. 13, fig. 4.
1847 *Ammonites Hambrovii* FORBES; FITTON, p. 299-300.
1850a *Ammonites Hambroviii* [sic] FORBES; d'ORBIGNY, p. 113.
1860 *Ammonites Hambrovii* FORBES; PICTET & CAMPICHE, p. 339.
1865 *Ammonites Arnaudi* COQUAND, p. 48, Pl. 2, figs. 1-2.
1906 *Ammonites Hambrovii* FORBES; SINZOW, p. 162-163.
1910 *Douvilleiceras Hambrovi* FORBES sp.; KILIAN, p. 341.
1915 *Douvilleiceras Hambrovii* FORBES sp.; KILIAN & REBOUL, p. 50.
1921 (1923) *Cheloniceras hambrovi* (FORBES); SPATH, p. 317, Pl. 8, fig. 3.
1927 *Douvilleiceras* cf. *Hambrovii* (FORBES); ROCH, Pl. 1, fig. 3.
1930 *Cheloniceras hambrovi* (FORBES); SPATH, p. 444-445 (pars).
1933 *Cheloniceras hambrovi* (FORBES); ROUCHADZE, p. 195.
1954 *Roloboceras hambrovi* (FORBES); CASEY, p. 114.
1957 *Roloboceras hambrovi* (FORBES); WRIGHT (*in* ARKELL *et alii*), p. L384-L385, fig. 501, 9.a-b.
1961b *Roloboceras hambrovi* (FORBES); CASEY, p. 179-182, text-figs. 55.a-b; Pl. 32, figs. 5.a-b.
1972 *Roloboceras* sp. ex. gr. *arnaudi* (COQUAND); SORNAY & MARIN, p. 108, Pl. B, fig. 4.
2006 *Roloboceras hambrovi* (FORBES); ROPOLO *et alii*, Pl. 11, fig. 2.

Material: three specimens : PRA1430, PRA1435 (ex ABR 1220: ROPOLO *et alii*, 2006, Pl. 11, fig. 2)

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1435	171	64	37.2	101	26	-	1.57	S/E
PRA1430	56	21	13.8	24	24	-	1.14	S/E

Description: Semi-evolute shell with very inflated whorls, increasing moderatly in height, wide-oval to subtrapezoidal whorl section, rounded venter, vertical umbilical wall, deep umbilicus. Ornament can consist of strong peri-umbilical tubercles becoming radially elongated bulges or strong nodes, each giving rise to one, two or three large strong ribs passing right on the venter. All ribs are equal, flattened and radial.

Discussion: According to CASEY (1961b, p. 180), ribbing, proportions, and tuberculation of *Roloboceras hambrovi* may have a wide range of variation. In our opinion, "*Ammonites*

Arnaudi", described and illustrated by COQUAND (1865, p. 48, Pl. 2, figs. 1-2) from a specimen collected by this author in the Aptian of Rosa (Aragon, Spain), but certainly idealized as was usual at that time, could be united with the species of FORBES. This taxon presents the general aspect of *Roloboceras hambrovi*, but differs in its more regular and stronger ribbing and a lesser number of umbilical tubercles. SORNAY & MARIN (1972, Pl. B, fig 4) figured a deteriorated shell that they named *Roloboceras* sp. ex. gr. *arnaudi*. These two specimens are within the range of variability in *Roloboceras hambrovi*.

Occurrence: *Deshayesites deshayesi* Zone (*Roloboceras hambrovi* Subzone), Comte Quarry section.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
C.104	90	35	32	~50	-	-	0.71 (d=50)	E

Description: Our specimen (originally described and figured by CONTE (1975, figs. 2-3) was identified by SORNAY (pers. comm. to G. CONTE) as belonging to the *Roloboceras transiens* group. It is a slightly compressed shell, with a semi circular whorl section. At D = 60 mm there are eight strong peri-umbilical tubercles and at D= 70 mm there are ten. On the last whorl, these tubercles become radially elongated bulges. Ribbing is not visible in the juvenile stage, but on the adult whorls each tubercle gives rise to a group of three thick blunt ribs passing on the venter.

Discussion: Our specimen shares some similarities with *Roloboceras hambrovi* (FORBES), but shows radial peri-umbilical tubercles forming prominent elongated nodes, which differ in shape from those of FORBES's species. In addition, its umbilical wall is higher and steeper in slope.

Occurrence: *Deshayesites deshayesi* Zone (*Roloboceras hambrovi* Subzone), Comte Quarry section.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1455	33.5	13	14	25.2	18	-	1.93	E

Description: Our specimen is conformable with that of figs. 5.a-b, Pl. 31 of CASEY (1961a). Very depressed juvenile whorls, massive tubercles similar to those of *Megatyloceras*, ending in strong main ribs. Between primary ribs are intercalated one, two or three secondary ribs devoid of tubercles. Deep umbilicus, coronate whorl section with spinose lateral tubercle.

Discussion: This form, rare at La Bédoule, is found in the Deshayesi Zone (Grandis Subzone). It has many similarities with *Cheloniceras royerianum* d'ORBIGNY, 1841, from the Furcata Zone. CASEY (1961b, p. 185) points out that *Roloboceras horridum* has an early *royerianum*-stage (the venter becomes smooth, without intercalary ribs), with a brief succeeding "*perli*" stage, followed by the characteristic "*horridum*" stage characterized by the obsolescence or enfeeblement of the ribbing, between two main ribs on the rounded venter. Some adult specimens may show an early loss of gross tubercles.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone (*Paradeshayesites grandis* Subzone), Comte quarry section.

Roloboceras sp. gr. *transiens* CASEY, 1961

(Pl. 8, fig. 2)

1961b *Roloboceras* (?) *transiens* sp. nov. CASEY, text-fig. 56 in p. 187.

1972 *Roloboceras* sp. ex. gr. *transiens* CASEY; SORNAY & MARIN, p. 108-109, Pl. C, fig. 4.

1975 *Roloboceras* sp. groupe *transiens* CASEY; CONTE, p. 105-110, figs. 2-3.

Material: One specimen : n° C.104

Roloboceras horridum (SPATH, 1930)

(Pl. 12, fig. 3)

1930 *Cheloniceras hambrovi* (FORBES) var. "*horrida*"; SPATH, p. 444.

1949 *Megatyloceras hambrovi* (FORBES) var. "*horrida*"; HUMPHREY, p. 149.

1954 *Roloboceras hambrovi* (FORBES) var. "*horrida*" SPATH; CASEY, p. 114.

1961b *Roloboceras horridum* (SPATH); CASEY, p. 185-186, Pl. 31, figs. 5.a-b; Pl. 32, figs. 1-4.

Material: One specimen, n° PRA1455

Roloboceras sp.

Material: a poorly preserved specimen, doubtfully identified as a half whorl of *Roloboceras* sp. N° PRA1411.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1411	92.5	35	30.2	18	12	-	0.51	E

Description: A crushed half whorl. Sculpture consists of twelve strong straight ribs with irregular disposition of peri-umbilical smooth tubercles. Umbilicus about one third of the diameter.

Discussion: This specimen in some respects is similar to *Roloboceras hambrovi* (FORBES), but its ribs are less numerous and more radial. It could be construed as a *Roloboceras hispanicum* var. *rotundatum* SORNAY & MARIN (1972), but this shell is preserved too poorly and its sculpture is too irregular for it to be attributed unreservedly to any species of *Roloboceras*.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone (*Roloboceras hambrovi* Subzone).

Genus *Megatyloceras* HUMPHREY, 1949

Type-species: *Douvilleiceras coronatum* ROUCHADZE 1933 (p. 195, fig. 12, Pl. 3, fig. 4).

Megatyloceras ricordeanum (d'ORBIGNY, 1850)

(Pl. 8, fig. 3; Pl. 9, fig. 4; Pl. 11, fig. 3)

1850 *Ammonites ricordeanum* d'ORBIGNY, Pl. 8, figs. 7-8.

1967 *Megatyloceras bonchevi* sp. n. DIMITROVA, p. 167, Pl. 85, fig. 1; Pl. 86, fig. 3.

Material: three complete specimens: PRA1424, C.865, PRA1425, some fragments.

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1424	78	21	26	77	20	-	3.66	E
C.865	70	18.8	22	63	24	-	3.35	E
PRA1425	65	17.2	19.8	60	20	-	3.48	E

Description: Very prominently tuberculated shell with very depressed coronate whorl section. Deep umbilicus; Uw is about 32 % of the diameter. Wide venter, feebly convex. Ribbing consists of pairs of primaries joining on either side to form one strong, thorn-like lateral tubercle, and includes two, three or four intercalated secondaries without tubercles. Spinose tubercles are located at wide intervals at the top of the umbilical wall.

Discussion: Although a comparison of *Megatyloceras ricordeanum* with *M. coronatum* (ROUCHADZE, 1933: p. 195, text-fig. 12; Pl. 3, fig. 4) is made difficult because the holotype of *M. coronatum* is incomplete, our specimens differ from ROUCHADZE's taxon in having a narrower umbilicus, a more prominent, sharper tuberculation, and a more depressed whorl section.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone (*Roloboceras hambrovi* Subzone).

Megatyloceras sp. aff. *coronatum* (ROUCHADZE, 1933)

1933 *Douvilleiceras coronatum* ROUCHADZE, p. 195, Fig. 12, pl. 3, fig. 4.

1972 *Megatyloceras coronatum* (ROUCHADZE) var. *ibericum* SORNAY & MARIN p. 11, Pl. B, figs. 1-2; Pl. D, figs. 4 & 8.

2005 *Megatyloceras coronatum* (ROUCHADZE); KOTETISHVILI *et alii*, p. 386, Pl. 95, figs. 3a-3b.

Material: a distorted half whorl: n° PRA1483

Measurements:

specimen	D	Wh	Uw	Wb	K	Ph	Wb/Wh	morphotype
PRA1483	113	~33	-	87.8	~18	-	2.66	E

Description: Distorted coronatiform half whorl with a very flattened whorl section. Wide external region. Very deep and narrow umbilicus. Sculpture consists of groups of two or three strong straight ribs joining on each side to form a sort of bulla or a strong elongated tubercle at the top of a steep umbilical wall. Between two tubercles appears one or two intercalated secondary ribs similar to the main ribs, but not tuberculated.

Discussion: This form differs from *Megatyloceras ricordeanum* in the shape of its whorl and in its tuberculation: the whorl section is less depressed and more subtrapezoidal; the tubercles are more discrete.

Occurrence: Lower Aptian, *Deshayesites deshayesi* Zone (*Roloboceras hambrovi* Subzone).

4. Conclusion

This study of the Douvilleiceratidae from the Lower and middle Aptian of the Bedoulian stratotype area allowed us to determine the precise stratigraphic position and succession of every group of this important Aptian ammonite family. The Lower and middle Aptian sequence is characterized by five successive genera (or subgenera):

- *Prochelonicera*s (from *Martelites sarasini* to *Deshayesites weissi* zones),
- *Cheloniceras* (*Deshayesites deshayesi* Zone to the base of the *Epicheloniceras debile* Subzone),
- *Roloboceras* (*Deshayesites deshayesi* Zone),
- *Megatyloceras* (*Deshayesites deshayesi* Zone),
- *Epicheloniceras* (*Epicheloniceras martini* and *Parahoplites melchioris* zones).

These five groups share similar morphological features and have numerous affinities. Consequently, distinguishing between two large adult specimens of *Cheloniceras* and *Epicheloniceras* is quite difficult. The initial stages of the nuclei are often identical. There is a common "*royerianum*" stage between the last representatives of *Cheloniceras* and of the first *Epicheloniceras*. Juveniles pose particular problems and because of these similarities, it is not always easy to recognize forms transitional between two genera. Their evolution seems generally to be progressive, particularly within the beds transitional from the uppermost Bedoulian to the lower Gargasian. Provisionally, we have chosen the first appearance of the genus *Epicheloniceras* to be an important biostratigraphical marker for the base of the middle Aptian. However, this datum must be confirmed. So we recommend that the extinction of the genus *Dufrenoyia* also be considered for this purpose. Finally we propose here an updated biozonation for the Lower / middle Aptian of the Cassis-La Bédoule area (Fig. 6). Several stratigraphic markers, already defined in other regions (CASEY *et alii*, 1998) have been identified at Cassis-La Bédoule, such as *Roloboceras hambrovi* (FORBES)*, *Cheloniceras meyendorffi* (d'ORBIGNY), *Epicheloniceras debile* CASEY, *Epicheloniceras gracile* CASEY, *Epicheloniceras buxtorfi* (JACOB). The recognition of these subdivisions facilitates correlations with the Boreal realm.

* Although at Cassis-La Bédoule this species appears to be a marker of the middle upper Bedoulian, in southern England it is restricted to the upper lower Bedoulian.

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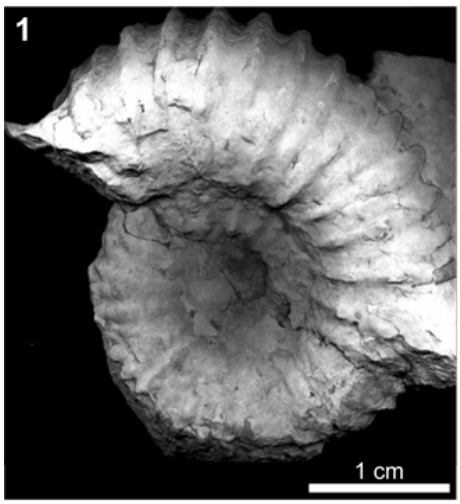
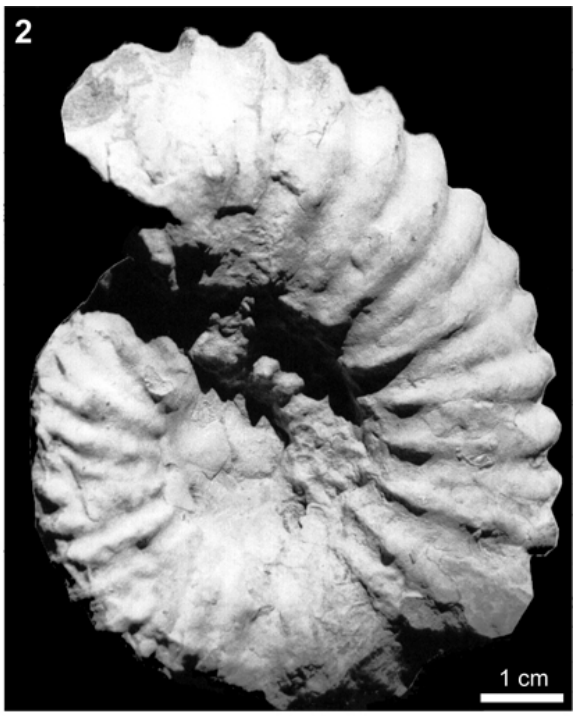




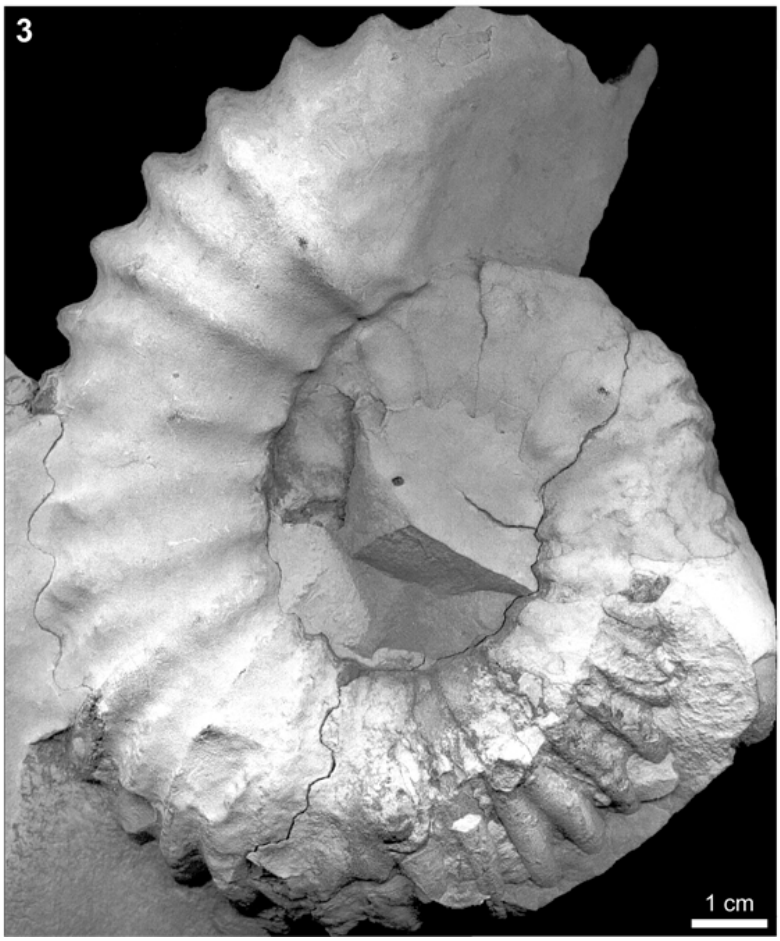


Plate 1:

1) *Prochelonicera pachystephanum* (UHLIG), n° PRB0419, bed 47, Upper Barremian, Waagenoides Zone – Le Brigadan section.
2) *Prochelonicera pachystephanum* (UHLIG), n° PRA1320, bed 64, Lower Aptian, Oglanlensis Zone – Les Caniers section.
3) *Prochelonicera pachystephanum* (UHLIG), n° PRA1322, bed 115, Lower Aptian, Weissi Zone – Les Fourniers section.

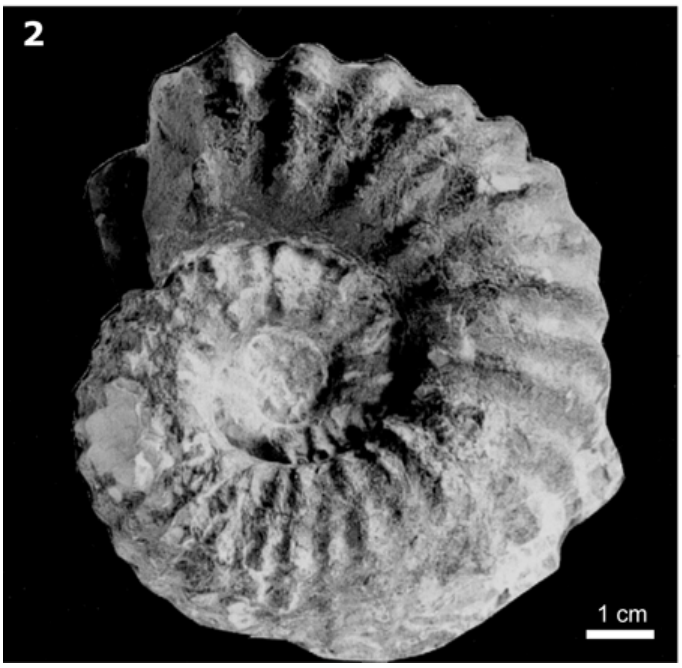


Plate 2:

1) *Prochelonicerasstobieskii* (d'ORBIGNY) n° Sc Dw301, Lower Aptian, Weissi Zone – La Bédoule, indetermined bed, in Université de Provence, Marseille St Charles, DEROGNAT Collection.
2) *Prochelonicerasalbrechtiaustriae* (HOHN.) *in* UHLIG, n° PRA1413, Lower Aptian, Weissi Zone – Les Fourniers section, bed 117.
3) *Prochelonicerasalbrechtiaustriae* (HOHN.) *in* UHLIG, n° PRA1414, Lower Aptian, Weissi Zone – Les Fourniers section, bed 114.

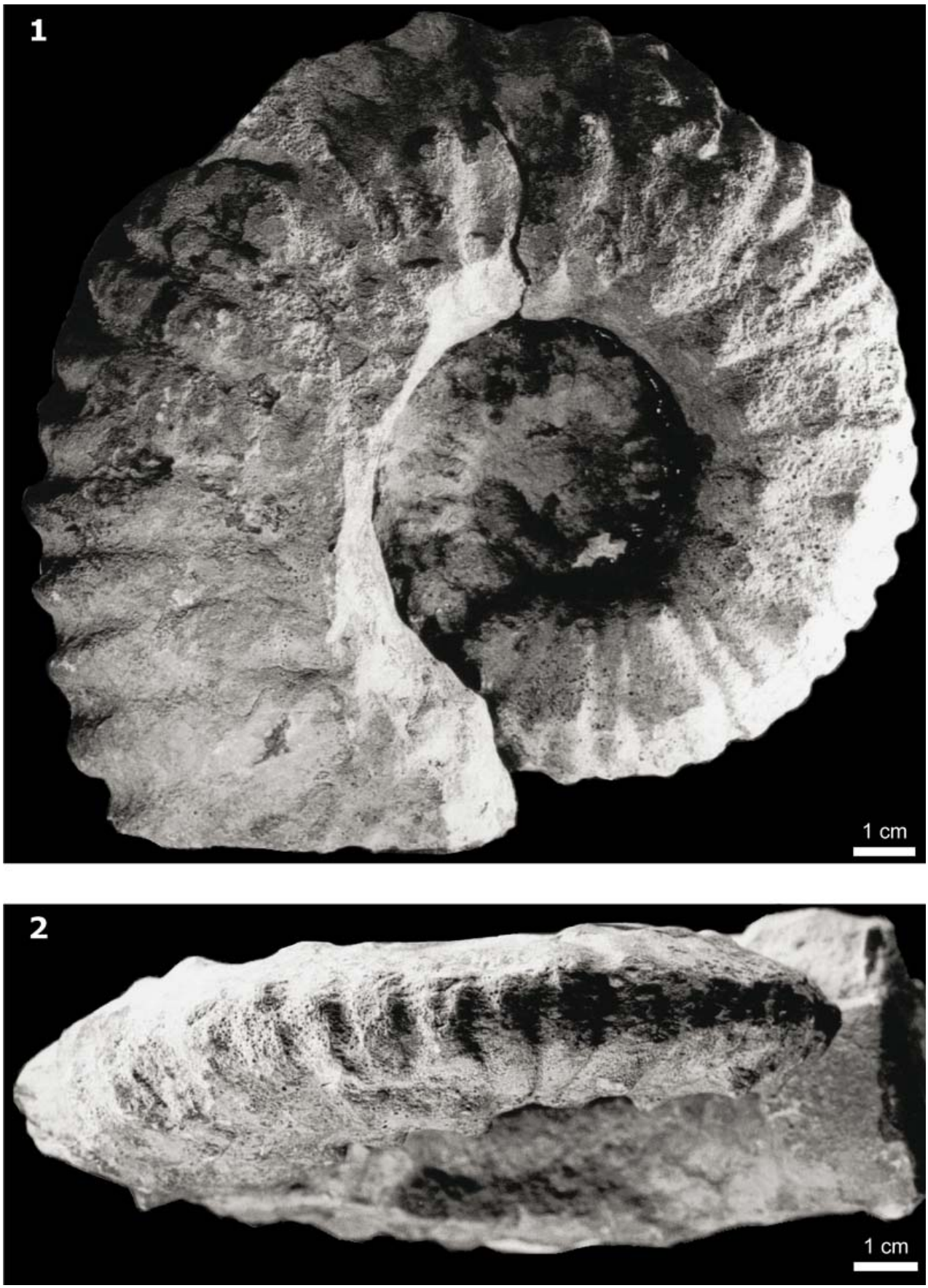
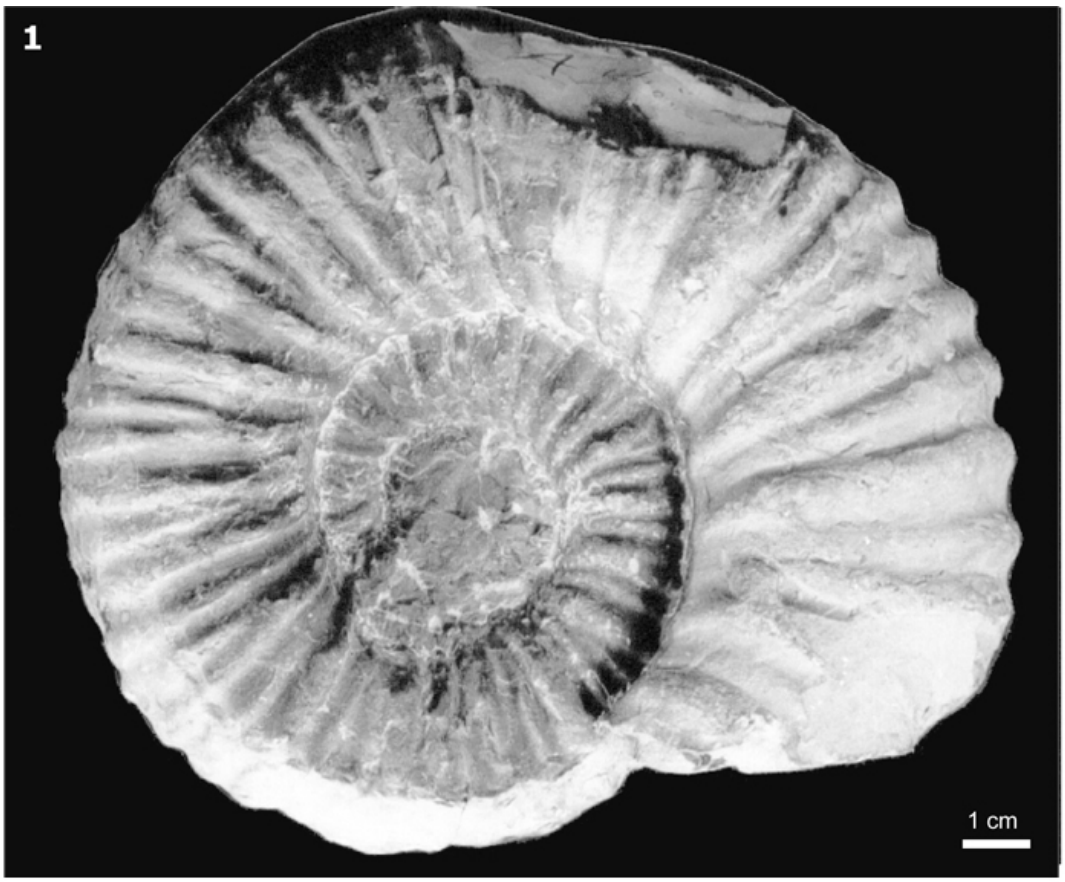


Plate 3:

1) *Prochelonicerasalbrechtiaustriae* (HOHN.) *in* UHLIG, n° Sc Dw403, Lower Aptian, Weissi Zone – La Bédoule, indetermined bed, in Université de Provence, Marseille St Charles, DEROGNAT Collection.
2) Same specimen, ventral view.



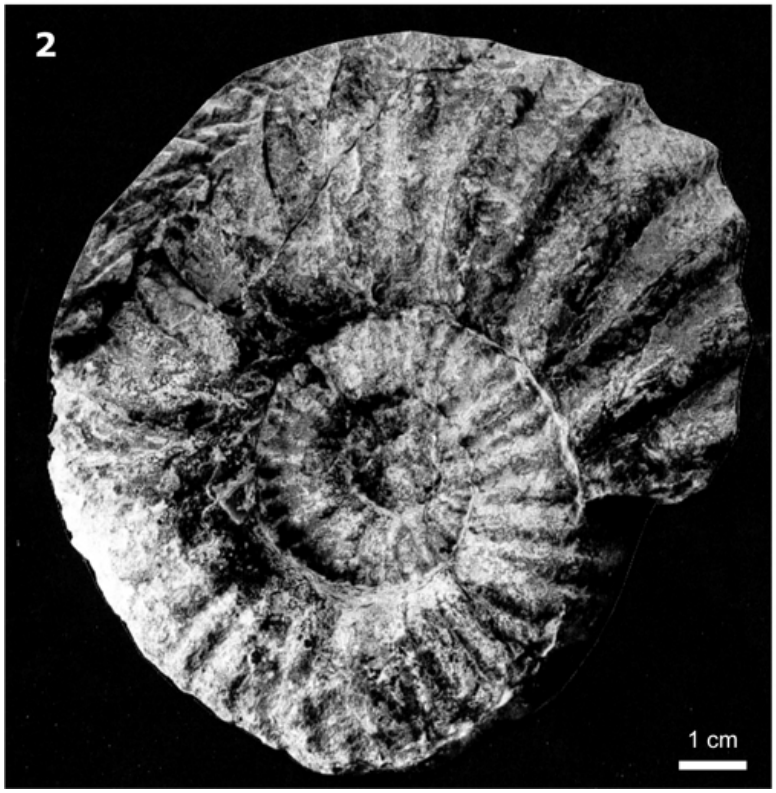


Plate 4:

1) *Prochelonicerasdechauxi* (KILIAN & REBOUL), n° Sc Dw302, Lower Aptian, Weissi Zone – La Bédoule, indetermined bed, in Université de Provence, Marseille St Charles, DEROGNAT Collection.
2) *Prochelonicerasalbrechtiaustriae* (HOHN.) *in* UHLIG, n° PRA1412, Lower Aptian, Weissi Zone – Les Fourniers section, bed 112.
3) *Prochelonicerasdechauxi* (KILIAN & REBOUL), n° PRA1422, Lower Aptian, Weissi Zone – Les Fourniers section, bed 116.

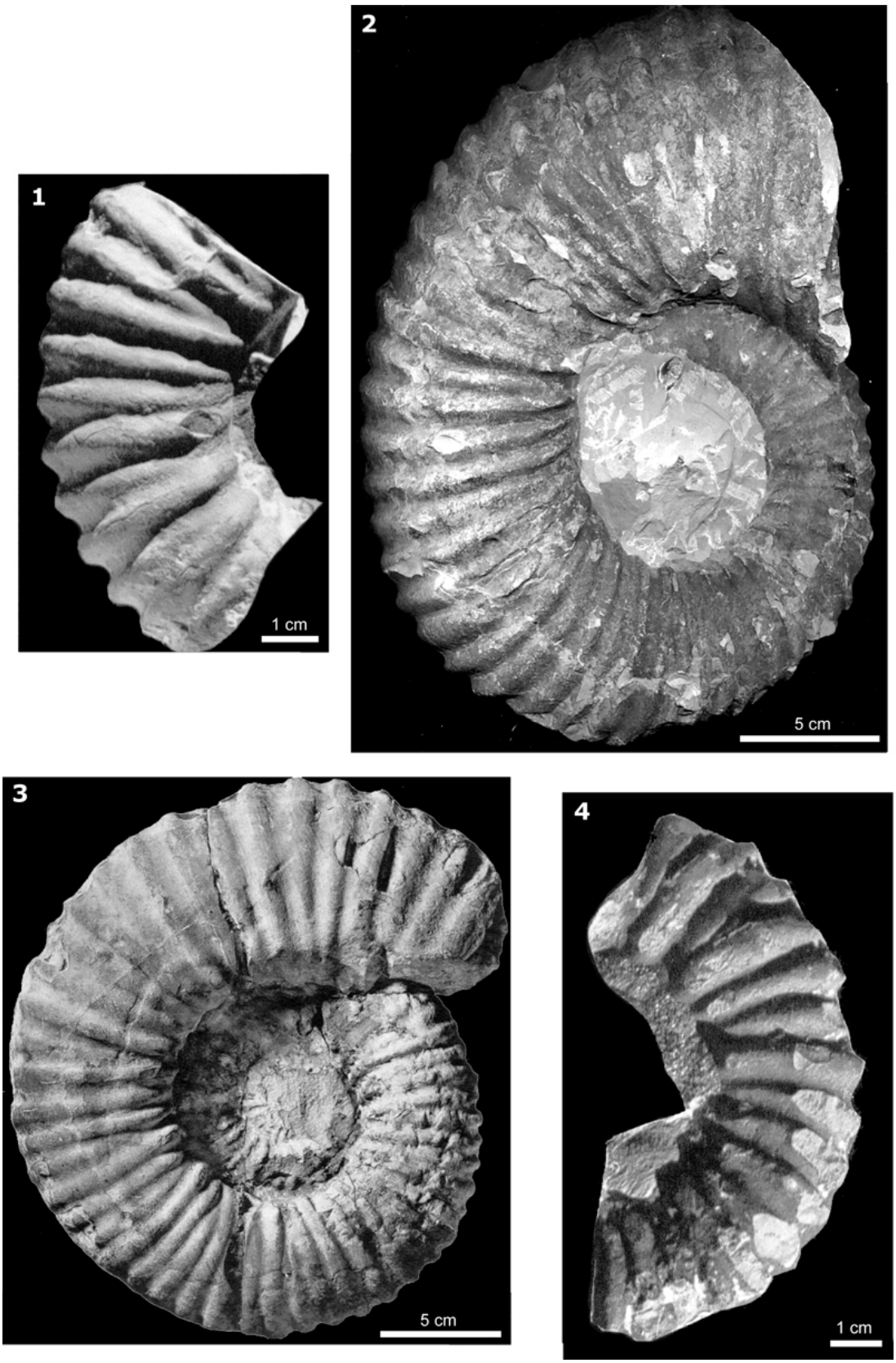


Plate 5:

1) *Prochelonicerasstobieskii* (d'ORBIGNY) sensu ROCH 1927, n° PRA1418, Lower Aptian, Weissi Zone, La Bédoule, Les Fourniers section, bed 115.
2) *Prochelonicerasstobieskii* (d'ORBIGNY) n° PRA1417, bed 116, Lower Aptian, Weissi Zone, La Bédoule, Les Fourniers section.
3) *Prochelonicerasalbrechtiaustriae* (HOHN.) var. *stobieskii* (d'ORBIGNY), La Bédoule, in ROCH, 1927, Pl. 2, fig. 1.
4) *Prochelonicerasstobieskii* (d'ORBIGNY) n° PRA1421, Lower Aptian, Weissi Zone, La Bédoule, Les Fourniers section, bed 121.

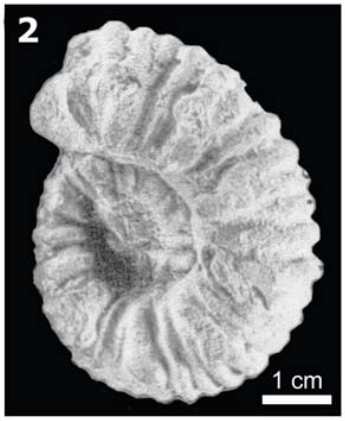


Plate 6:

1) *Cheloniceras crassum* SPATH - Université de Provence, Marseille-St. Charles, DEROGNAT Collection, n° Sc Dw12609 - Lower Aptian, Deshayesi Zone, La Bédoule, indetermined bed (labeled D5).
2) *Roloboceras hambrovi* (FORBES), n° PRA1430, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section, bed 148.
3) *Cheloniceras crassum* SPATH - n° C.821, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section bed 170a.

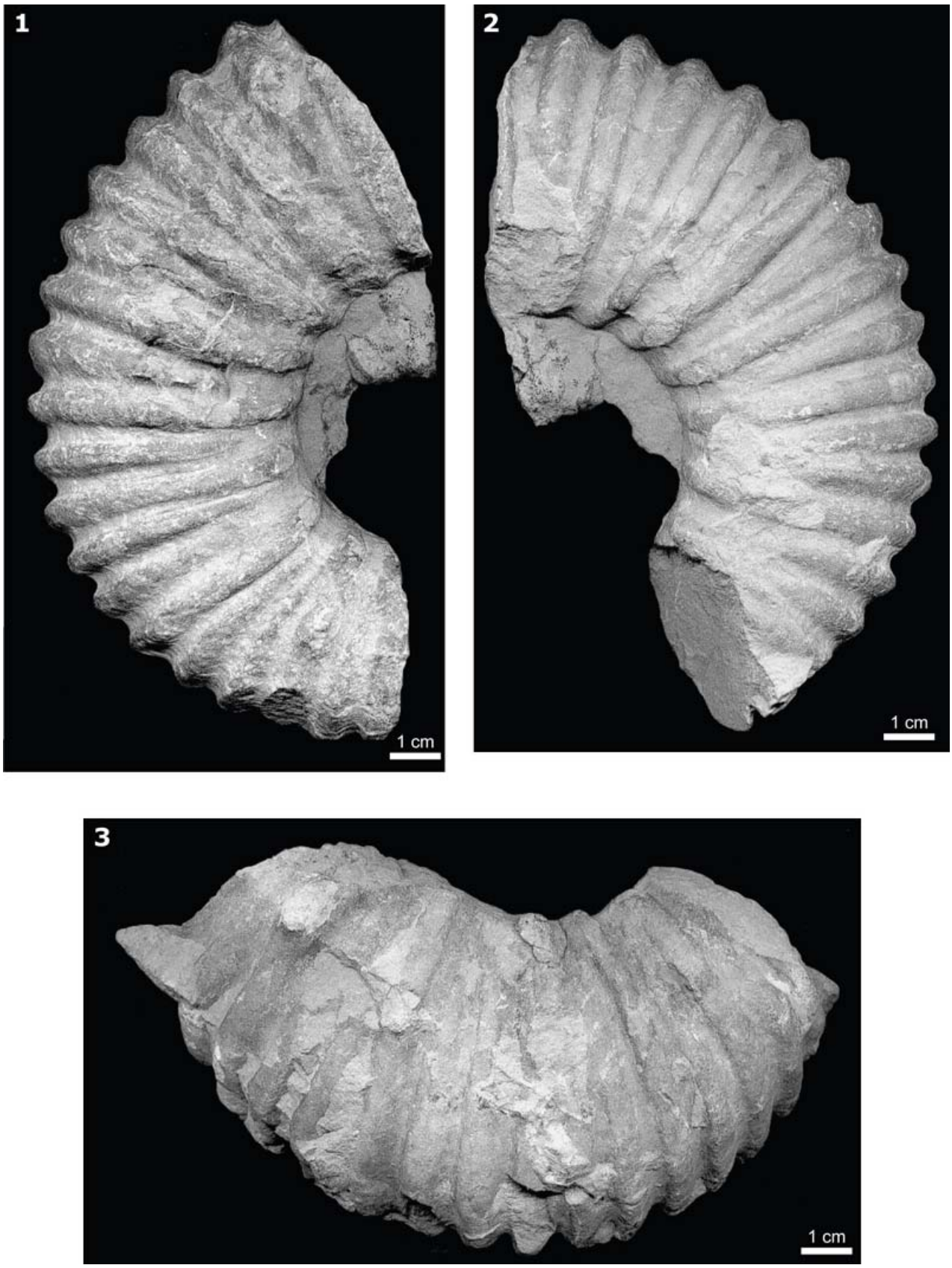


Plate 7:

1-2) *Cheloniceras crassum* SPATH – n° C.861, Lower Aptian, Deshayesi Zone, Comte quarry section, bed 166.
3) *Cheloniceras crassum* SPATH, n° C.859, bed 168, Lower Aptian, Deshayesi Zone, Comte quarry section, bed 168.

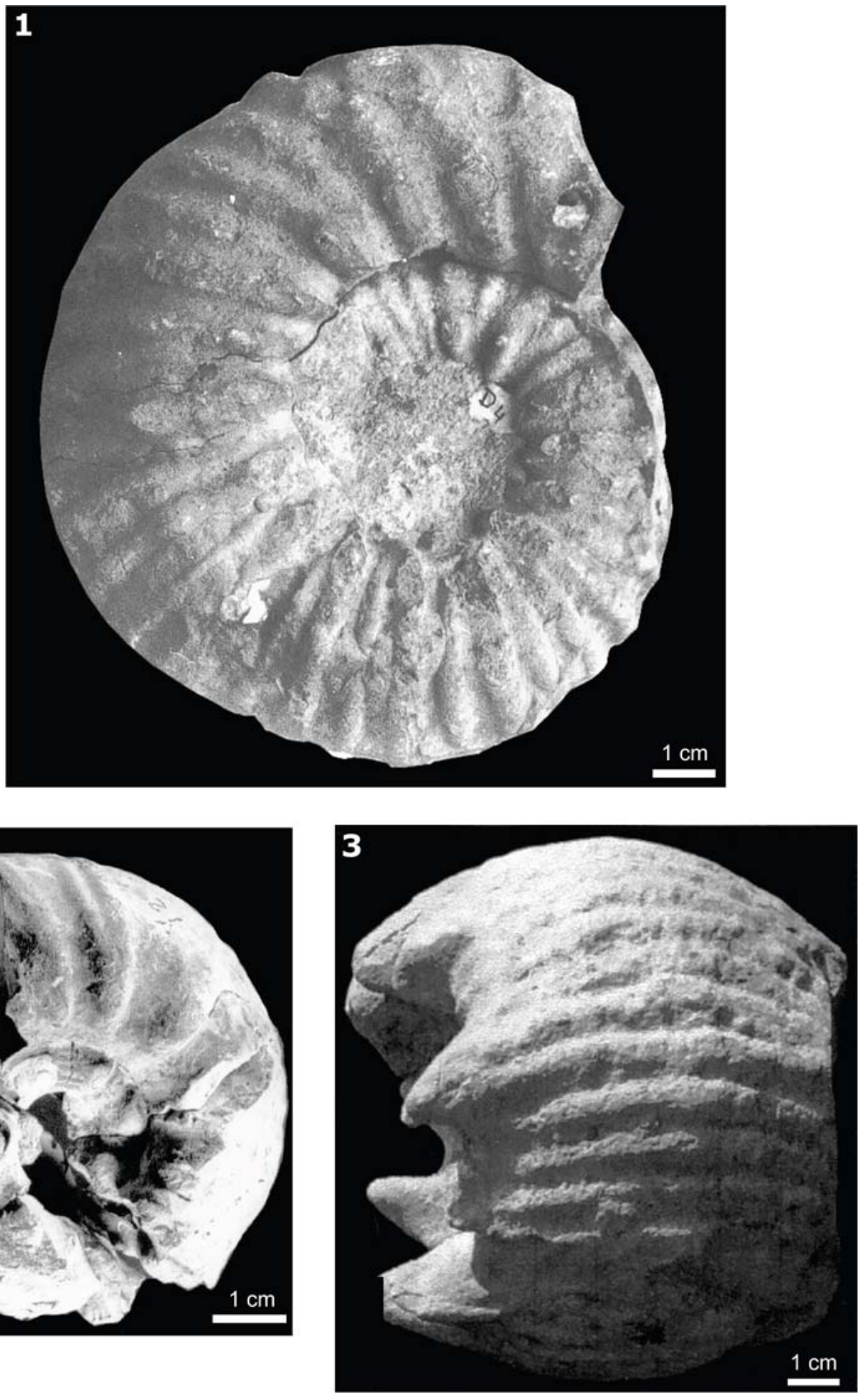


Plate 8:

1) *Cheloniceras kiliani* (KOENEN 1902) – n° SC 12900, Lower Aptian, Deshayesi Zone, Cassis-La Bédoule, probably Comte quarry section, indetermined bed, DEROGNAT Collection (labeled D4).
2) *Roloboceras* sp. gr. *transiens* CASEY 1961 – n° C.104, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section, bed 150.
3) *Megatyloceras ricordeanum* (d'ORBIGNY) – n° PRA1424, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section, bed 150.

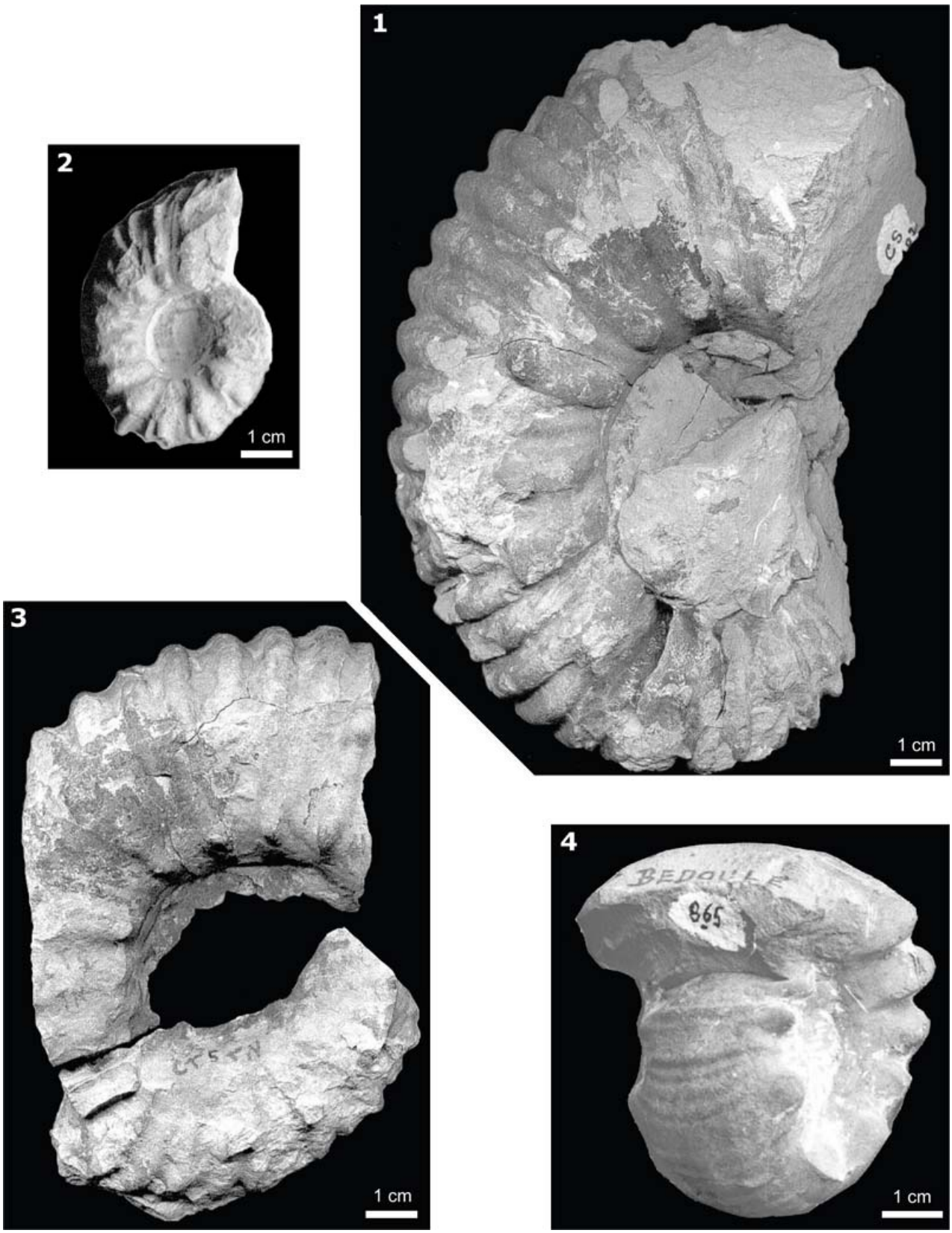


Plate 9:

1) *Cheloniceras parinodum* CASEY – n° C.102(right side), Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 170.
2) *Cheloniceras disparile* CASEY - n° PRA1452, Lower Aptian, Deshayesi Zone, Grandis Subzone e, Comte quarry section, bed 169.
3) *Cheloniceras parinodum* CASEY – n° C.103, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 166.
4) *Megatyloceras ricordeanum* (d'ORBIGNY) – n° C.865, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section, bed 158.

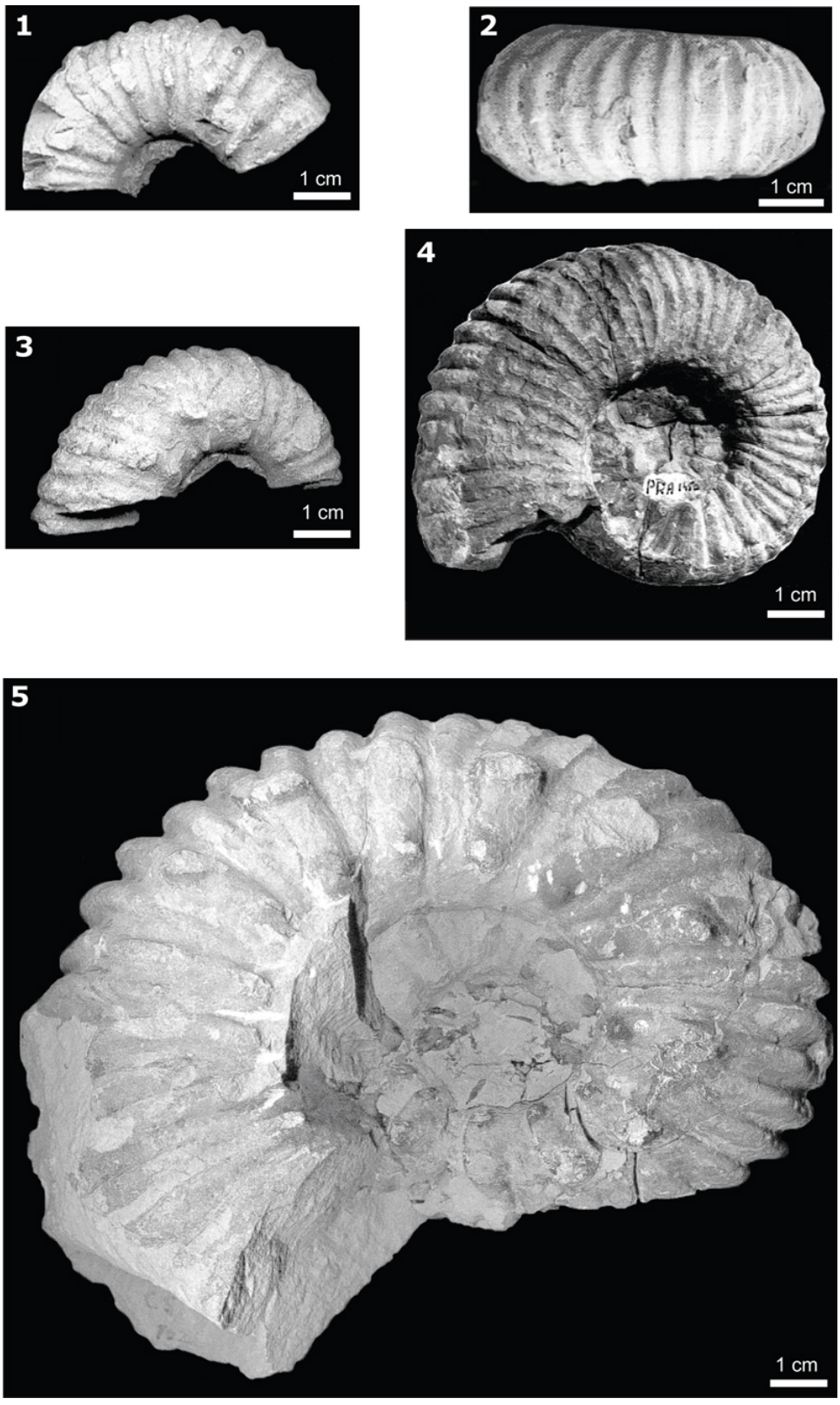


Plate 10:

1-3) *Cheloniceras seminodosum* (SINZOW), n° C.868, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 165.
2) *Cheloniceras seminodosum* (SINZOW), n° C.869, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 166.
4) *Cheloniceras seminodosum* (SINZOW), n° PRA1450, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 166.
5) *Cheloniceras parinodum* CASEY – n° C.102 (left side), Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 170.

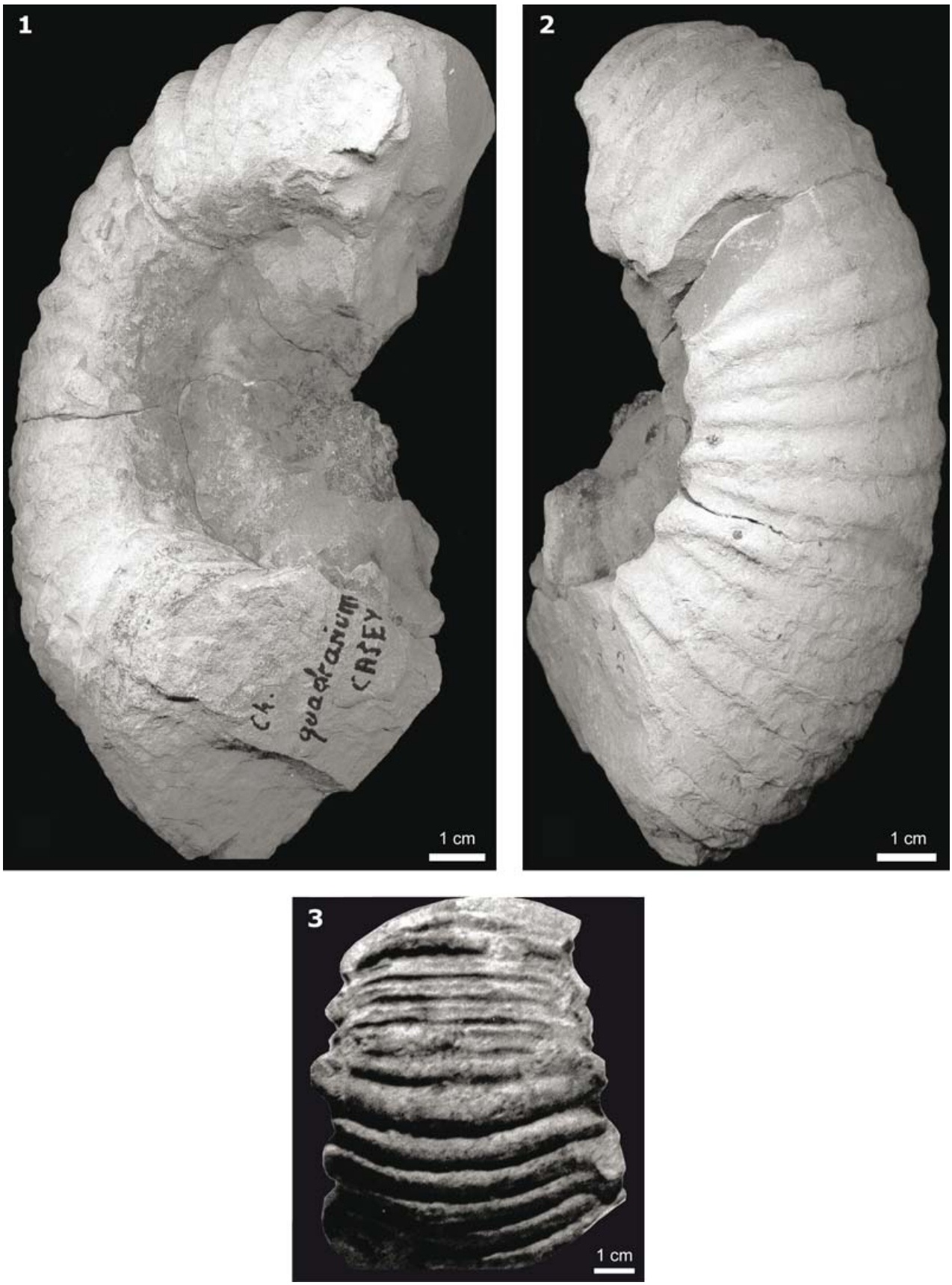


Plate 11:

1-2) *Cheloniceras quadrarium* CASEY - n° C.912, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 168.
3) *Megatyloceras ricordeanum* (d'ORBIGNY) PRA1425, Lower Aptian, Deshayesi Zone, Hambrovi Subzone, Comte quarry section, bed 158.

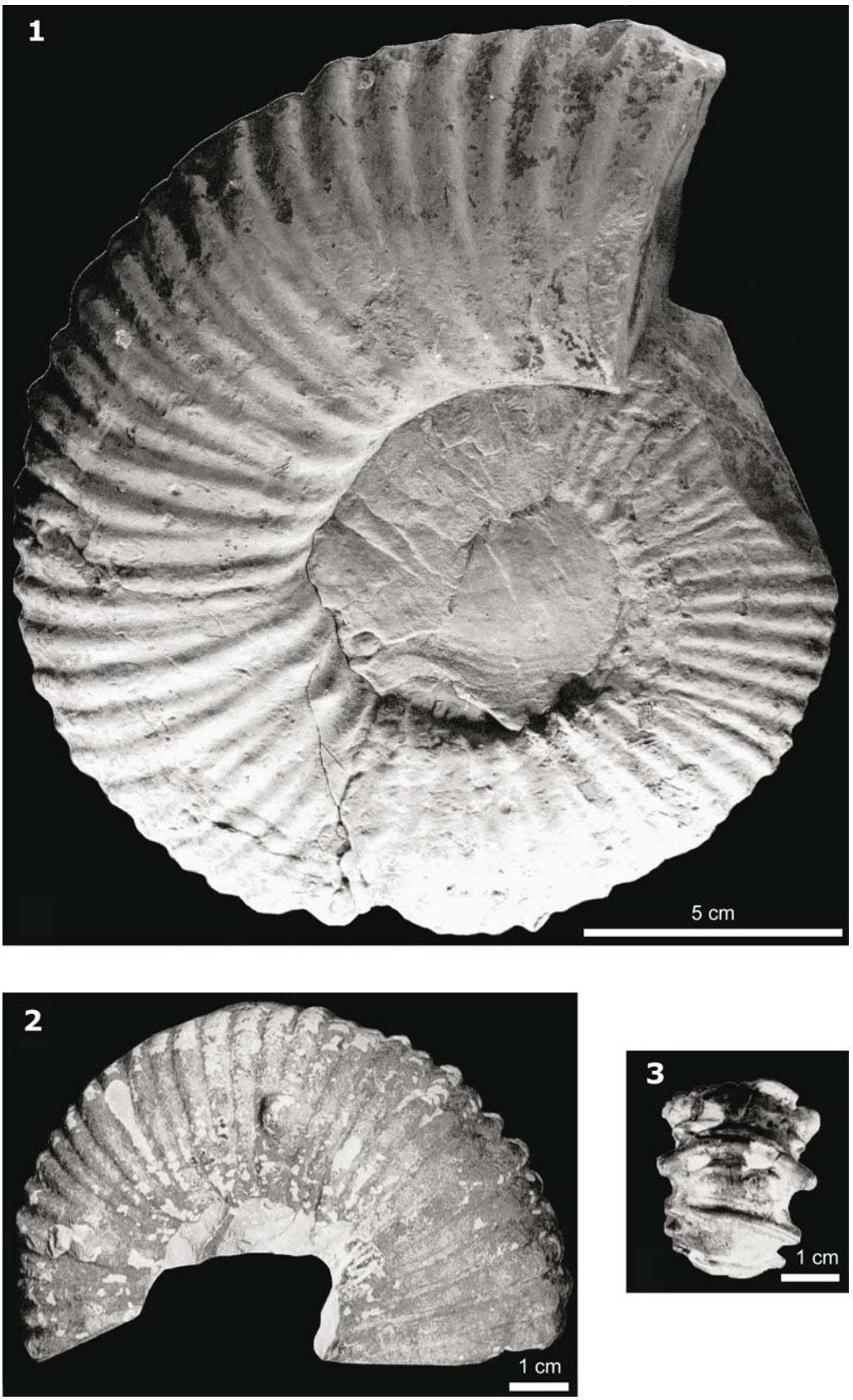
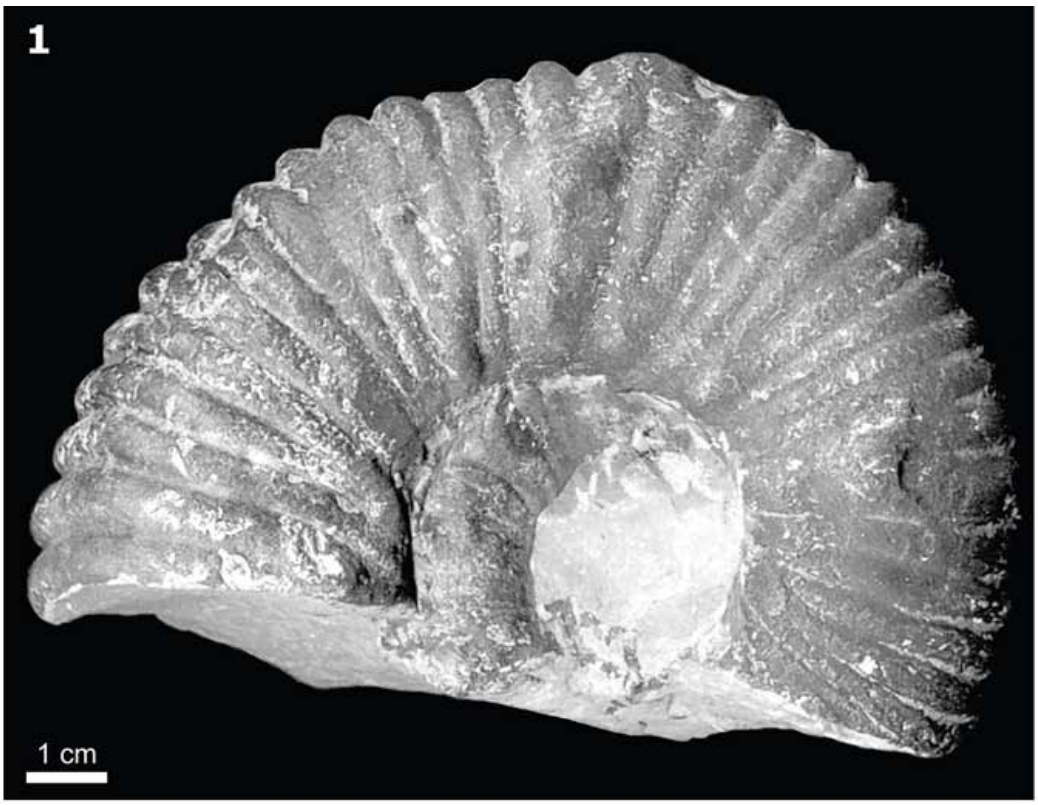


Plate 12:

1) *Cheloniceras mackesoni* CASEY (D: 355,5 mm) n° PRA1451, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 164.
2) *Cheloniceras meyendorffi* (d'ORBIGNY) n° C.872, Lower Aptian, Furcata Zone, Comte quarry section, bed 174.
3) *Roloboceras horridum* CASEY, small specimen, n° PRA1455, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 170.

Plate 13:

1) *Cheloniceras mackesoni* CASEY (D = 410 mm) n° PRA1452, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 166.



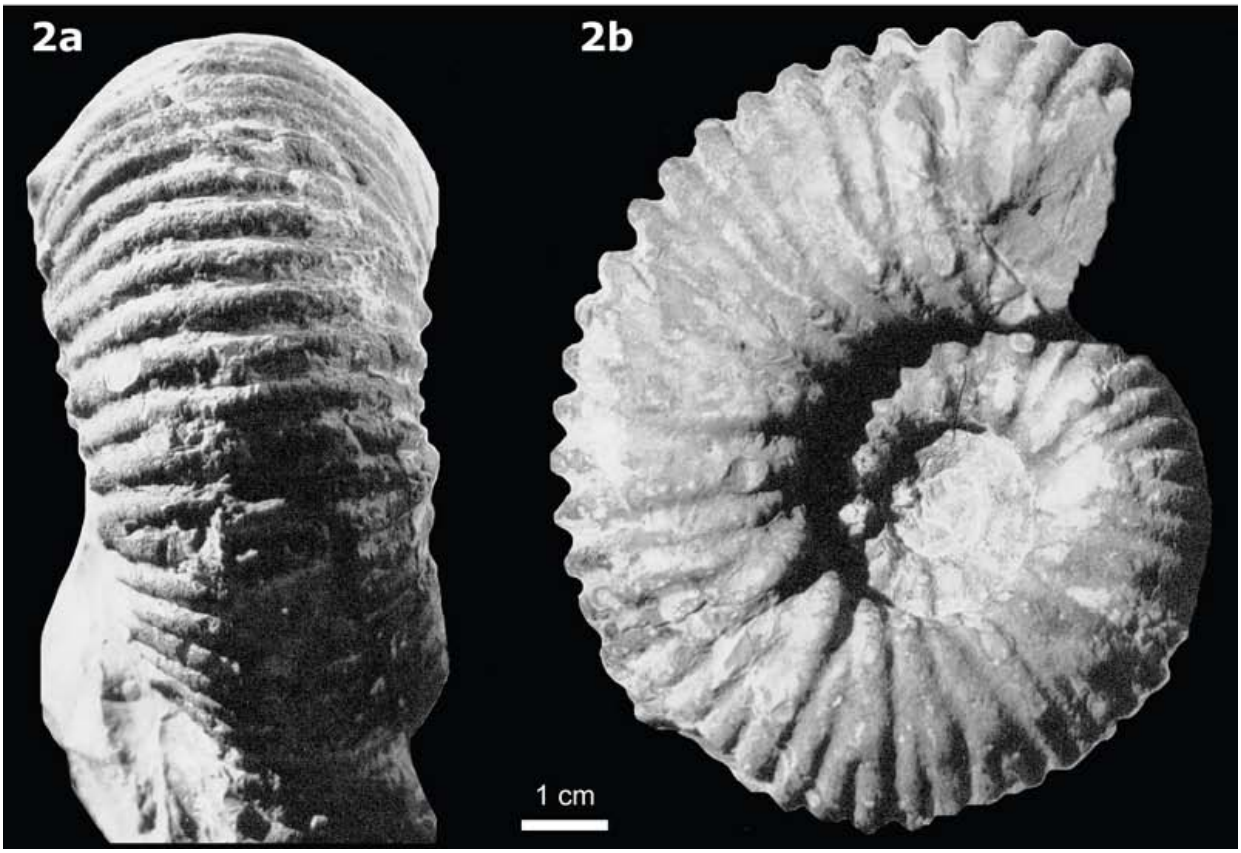
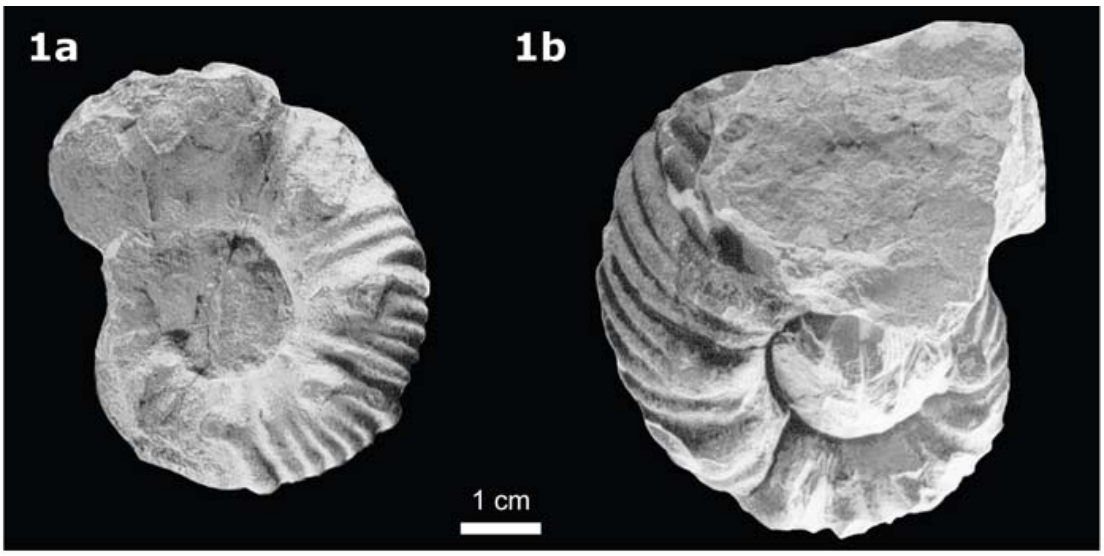


Plate 14:

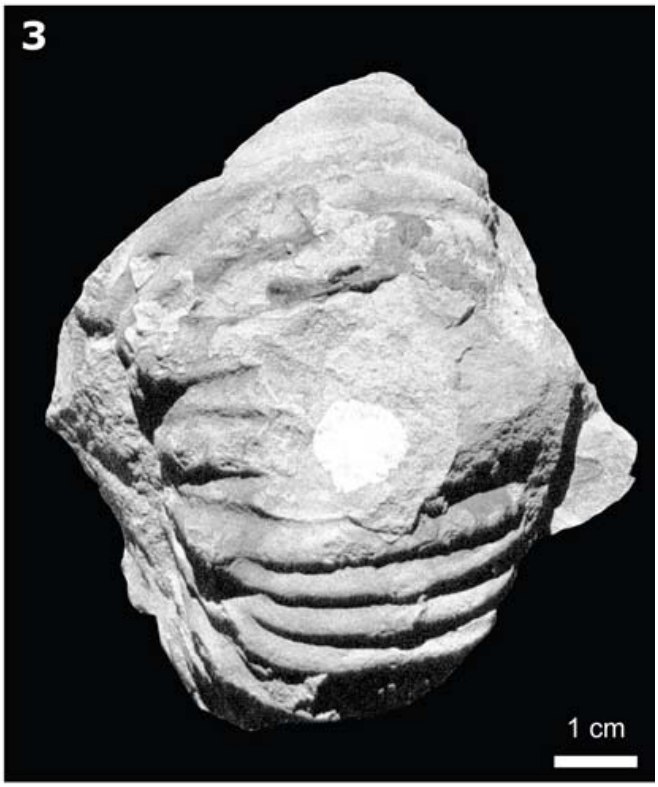
1) *Cheloniceras meyendorffi* (d'ORBIGNY), n° PRA1460, Lower Aptian, Furcata Zone, Comte quarry section, bed 176.
2.a-b) *Cheloniceras cornuelianum* (d'ORBIGNY) n° PRA1456, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 166.

Plate 15:

1.a-b) *Cheloniceras cornuelianum* (d'ORBIGNY) n° C.874 (1.a) & C.875 (1.b), Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 162 (1.a), bed 166 (1.b).
2) *Cheloniceras cornuelianum* (d'ORBIGNY) n° C.876, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 169.
3) *Cheloniceras cornuelianum* (d'ORBIGNY) n° C.877, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 169.
4) *Cheloniceras minimum* CASEY, n° C.878, Lower Aptian, Furcata Zone, Comte quarry section, bed 171.
5) *Cheloniceras seminodosum* (SINZOW) n° C.880, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 164.
6) *Cheloniceras seminodosum* (SINZOW) n° C.881, Lower Aptian, Deshayesi Zone, Grandis Subzone, Comte quarry section, bed 165.


1a
1b
1 cm


2
1 cm


3
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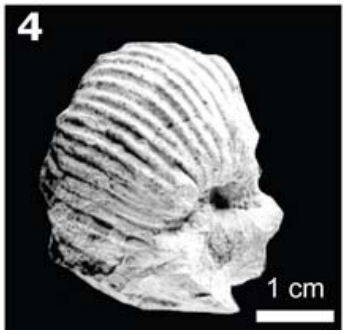
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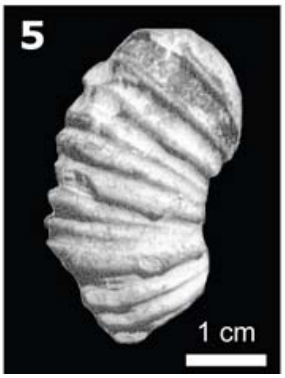
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1 cm

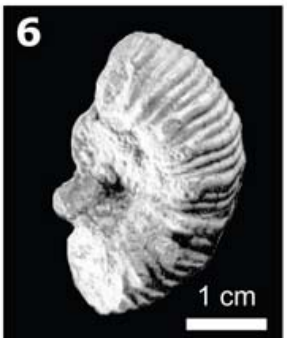
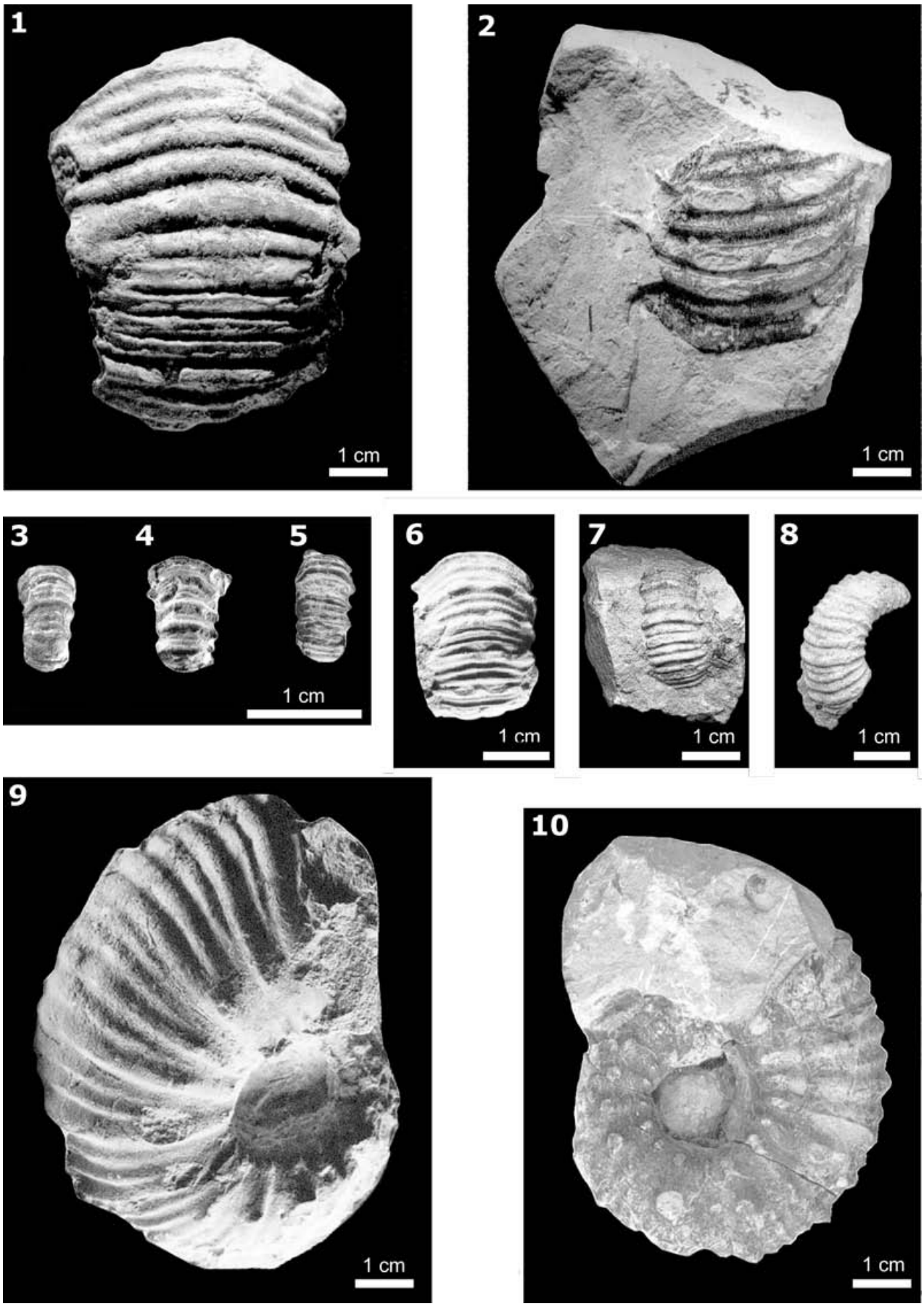

6
1 cm

Plate 16:

1) *Cheloniceras cornuelianum* (d'ORBIGNY) n° C.890, middle Aptian (Gargasian), Martini Zone, Comte quarry, bed 169.
2) *Epicheloniceras martini* var. *martinioides* CASEY, n° C.G. 901, middle Aptian (Gargasian), Martini Zone, La Marcouline section, bed 9.
3) *Epicheloniceras martini* (d'ORBIGNY) n° C.G. 903, middle Aptian (Gargasian), Martini Zone, La Marcouline section, bed 7.
4) *Epicheloniceras martini* (d'ORBIGNY) n° C.G. 902, middle Aptian (Gargasian), Martini Zone, La Marcouline section, bed 8.
5) *Epicheloniceras martini* (d'ORBIGNY) n° C.G. 905, middle Aptian (Gargasian), Martini Zone, La Marcouline section, bed 28.
6) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 1998 middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 78.
7) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 1997 middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 74.
8) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 1999 middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 64.
9) *Epicheloniceras martini* var. *martinioides* CASEY, n° C.G. 911, middle Aptian (Gargasian), Martini Zone, La Marcouline section, bed 10.
10) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 2000 middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 77.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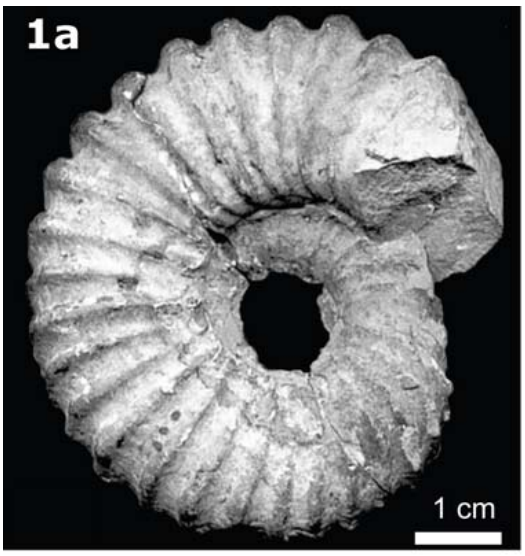
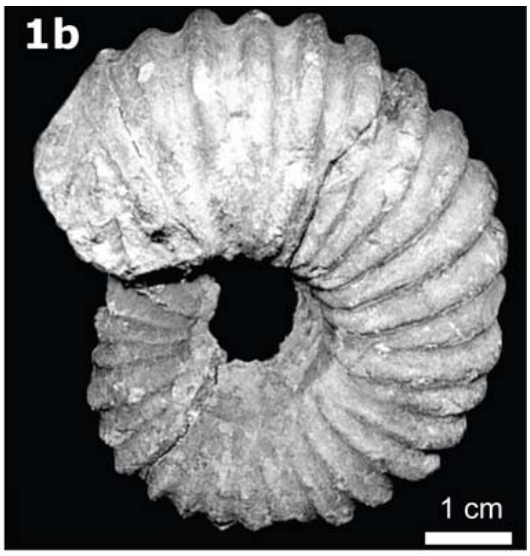




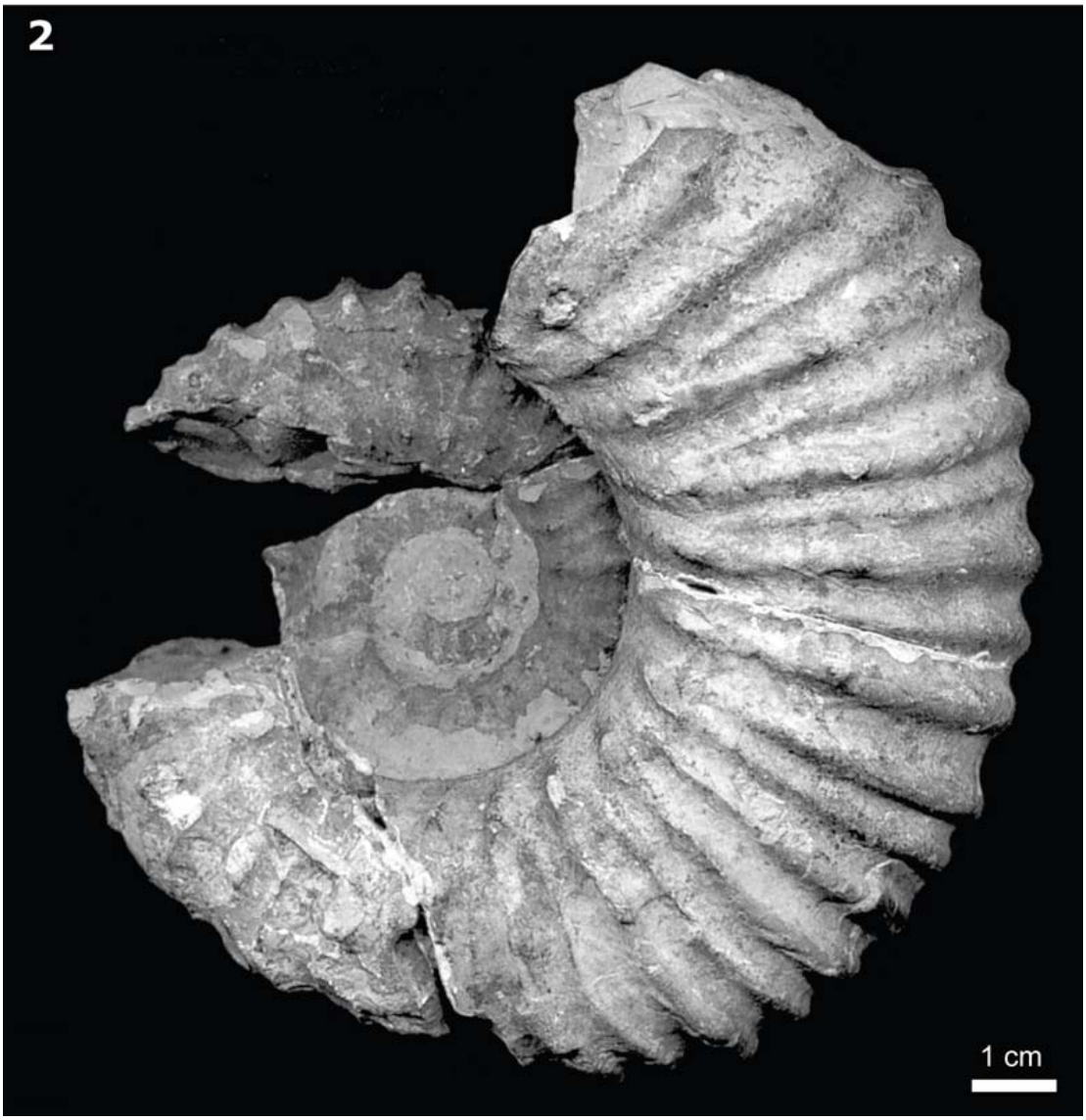


Plate 17:

1.a-b) *Epicheloniceras debile* CASEY, n° PRAG 1476, middle Aptian (Gargasian), Martini Zone, Debile Subzone, La Marcouline section, bed 8.
2) *Epicheloniceras debile* CASEY, n° PRAG 1482, middle Aptian (Gargasian), Martini Zone, Debile Subzone, La Marcouline section, bed 10.

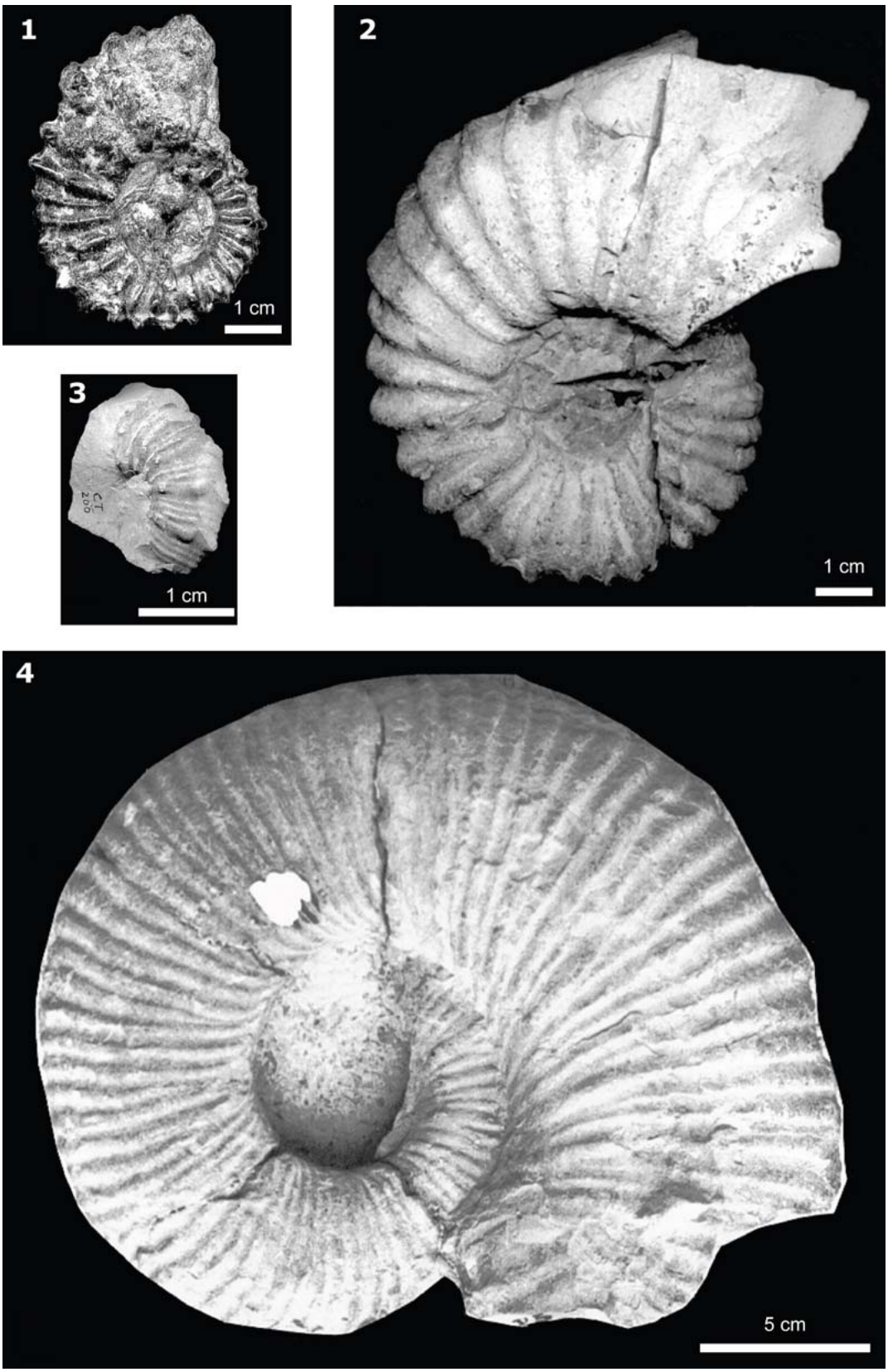


Plate 18:

1) *Epicheloniceras subnodosocostatum* (SINZOW), n° PRAG 1477, middle Aptian (Gargasian), Martini Zone, Debile Subzone, La Marcouline section, bed 22.
2) *Epicheloniceras buxtorfi* (JACOB), n° PRAG 1510, middle Aptian (Gargasian), Martini Zone, Buxtorfi Subzone, La Marcouline section, bed 51.
3) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 1478; middle Aptian (Gargasian), Martini Zone, Buxtorfi Subzone, La Marcouline section, bed 61.
4) *Cheloniceras mackesoni* CASEY La Bédoule, probably Comte quarry section, indetermined bed, DEROGNAT Collection.

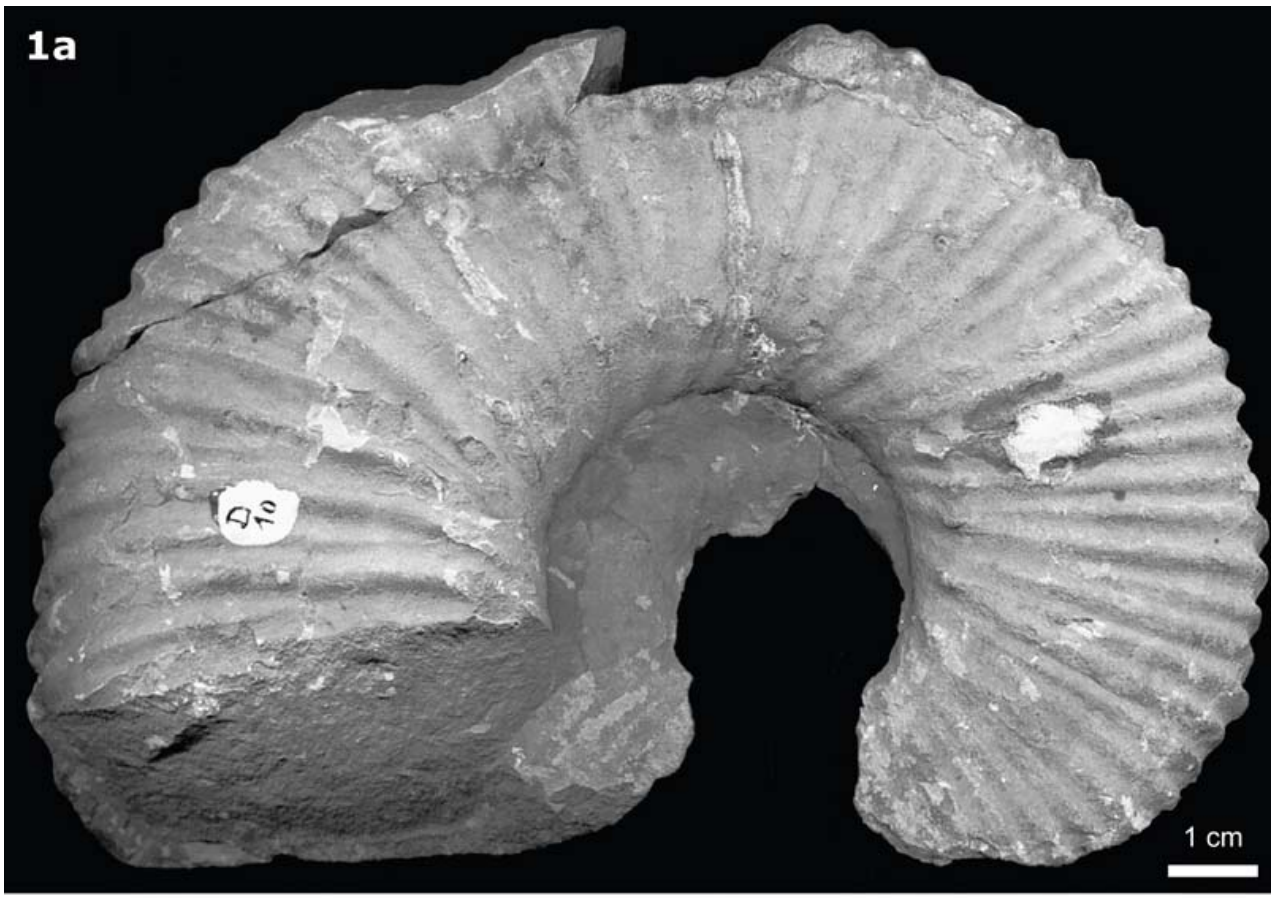


Plate 19:

1.a-b) *Epicheloniceras gracile* CASEY, La Bédoule, probably La Marcouline quarry section, undetermined bed, DEROGNAT Collection, labeled D10.

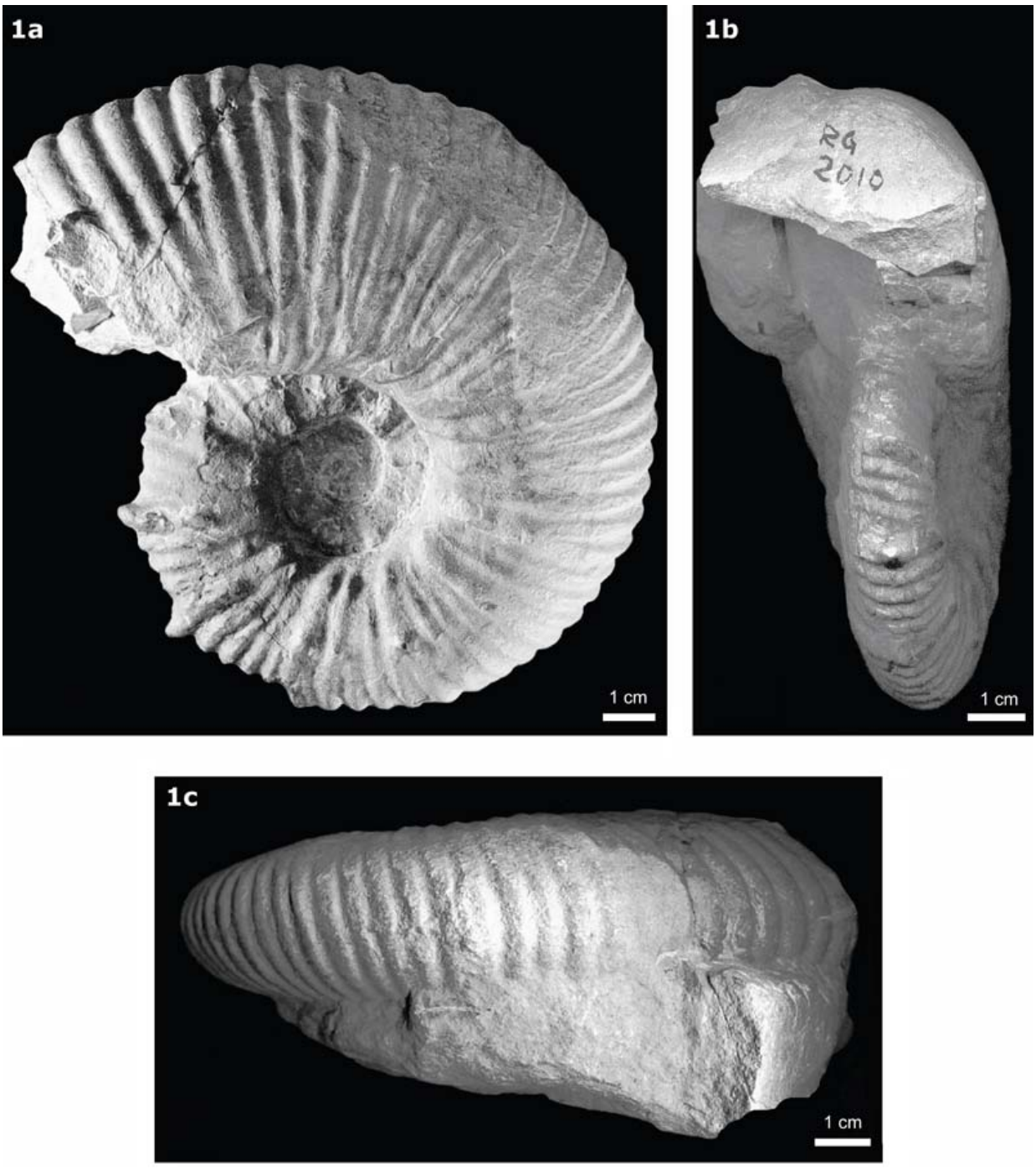
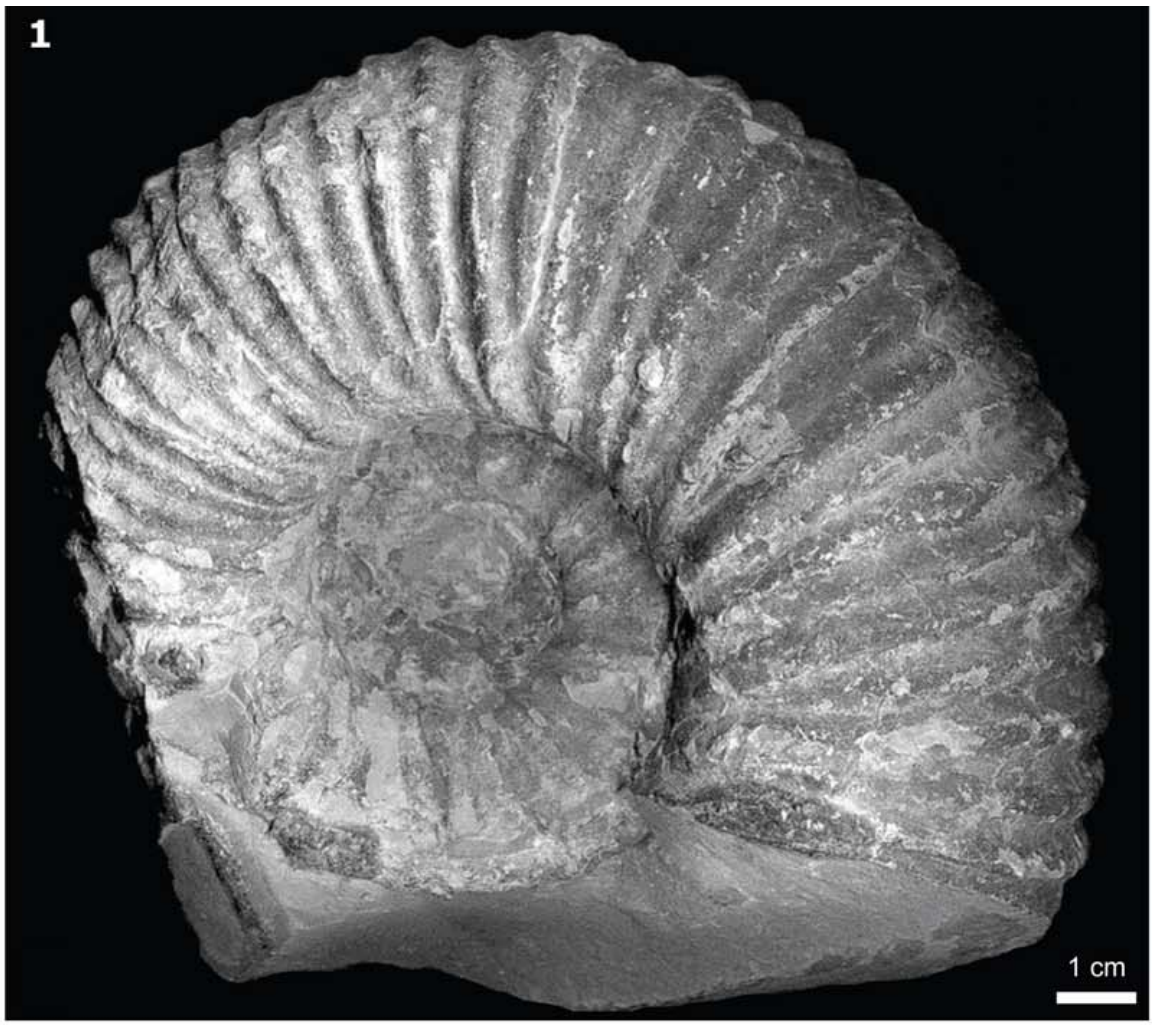


Plate 20:

1.a) *Epicheloniceras tschernyschewi* (SINZOW), n° RG2010 middle Aptian (Gargasian), Melchioris Zone, Fontblanche section (side view), bed 21. (GONNET Collection)
1.b) Same specimen (front view).
1.c) Same specimen (ventral view).

Plate 21:

1) *Epicheloniceras gracile*, n° PRAG 1490, middle Aptian (Gargasian), Martini Zone, Debile Subzone, La Marcouline section, bed 8.
2) *Epicheloniceras buxtorfi* (JACOB), n° PRAG 2011, ventral view middle Aptian (Gargasian), Martini Zone, Buxtorfi Subzone, La Marcouline section, bed 54.
3) *Epicheloniceras eotypicum* CASEY, n° PRAG 2017, middle Aptian (Gargasian), Martini Zone, Debile Subzone,, La Marcouline section, bed 26
4) *Epicheloniceras subnodosocostatum* (SINZOW) n° CG46, middle Aptian (Gargasian), Gracile Subzone, La Marcouline section, bed 44
5) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 2012, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 74.
6) *Epicheloniceras tschernyschewi* (SINZOW), n° PRAG 2014, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 76.
7-8) *Epicheloniceras eotypicum* CASEY, n° PRAG 2015, middle Aptian (Gargasian), Martini Zone, Debile Subzone, La Marcouline section, bed 26.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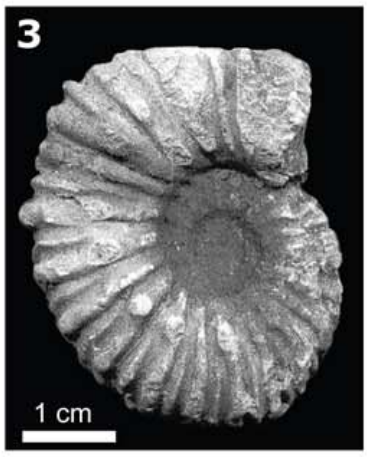
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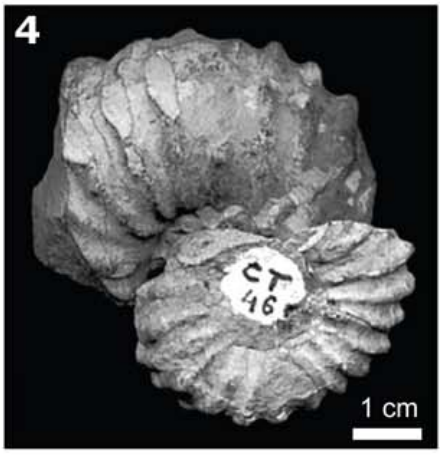
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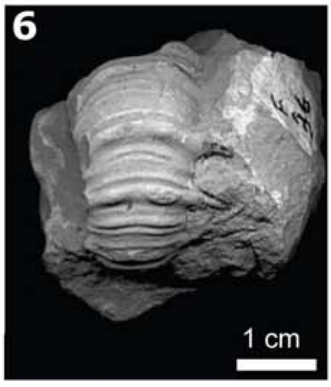
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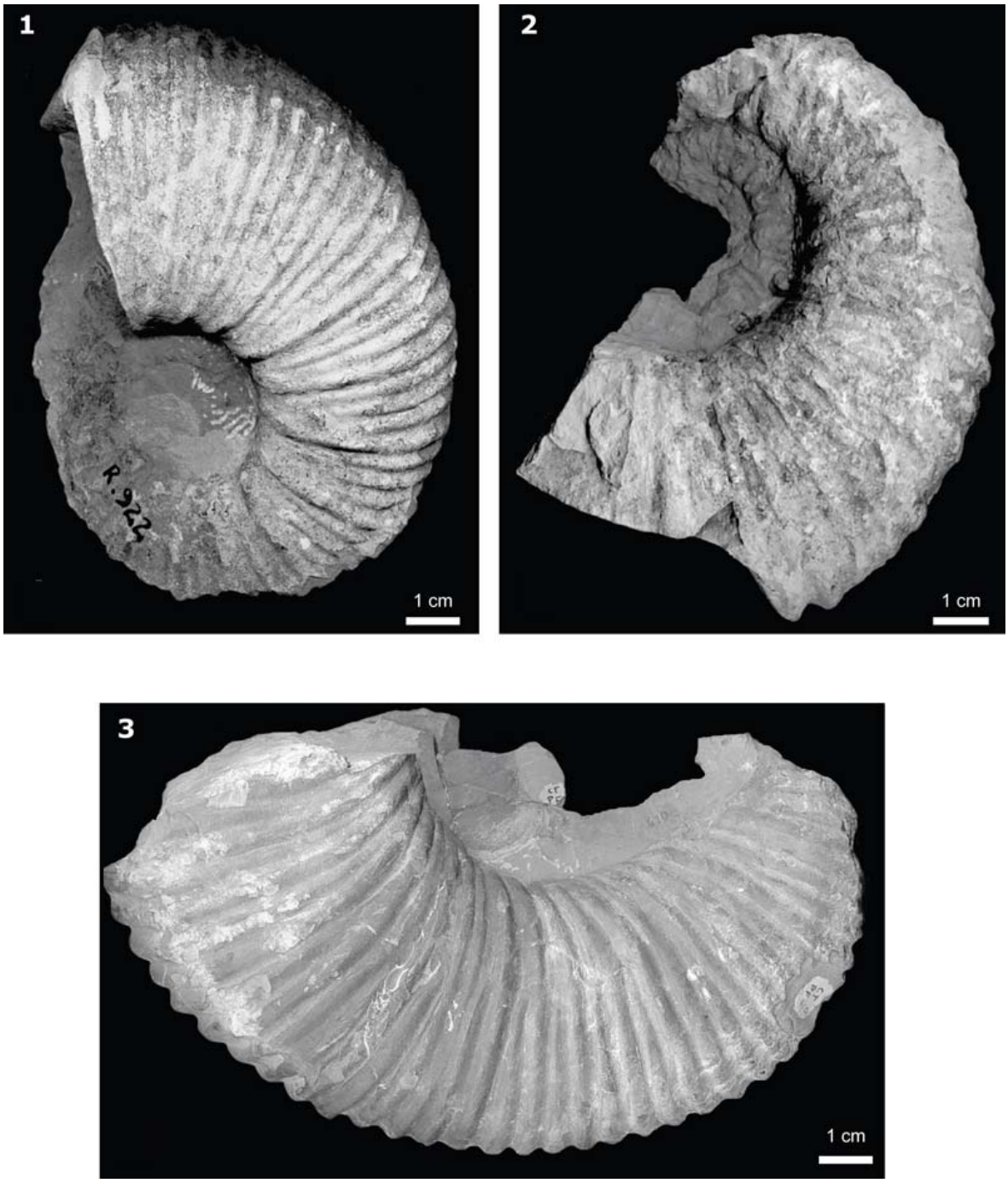

Plate 22:

1) *Epicheloniceras waageni* (ANTHULA), n° C.913, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 74.
2) *Epicheloniceras waageni* (ANTHULA), n° C.914, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 75.
3) *Epicheloniceras waageni* (ANTHULA), n° C.915, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 76.

▶Plate 23:

1) *Parahoplites flexisulcatus* (d'ORBIGNY), n° C.964, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 65.
2) *Parahoplites flexisulcatus* (d'ORBIGNY) *in* ROCH, Pl. 1, fig. 2, Aptien, La Bédoule, "marnes à *Parahoplites furcatus*" (?), p. 19.
3) *Acanthohoplites* sp., n° C.967, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 66 [no scale].


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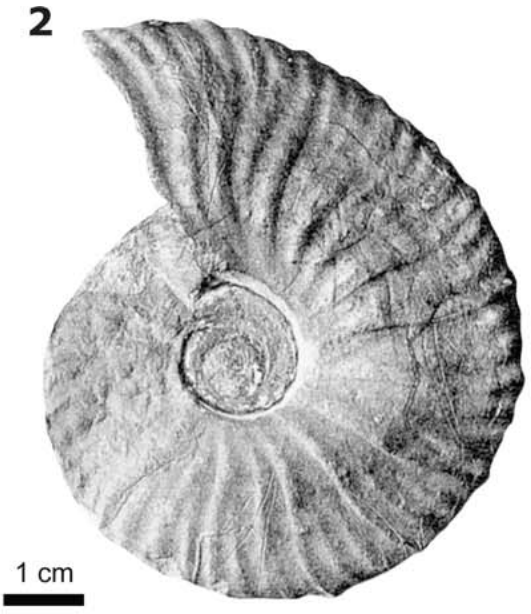
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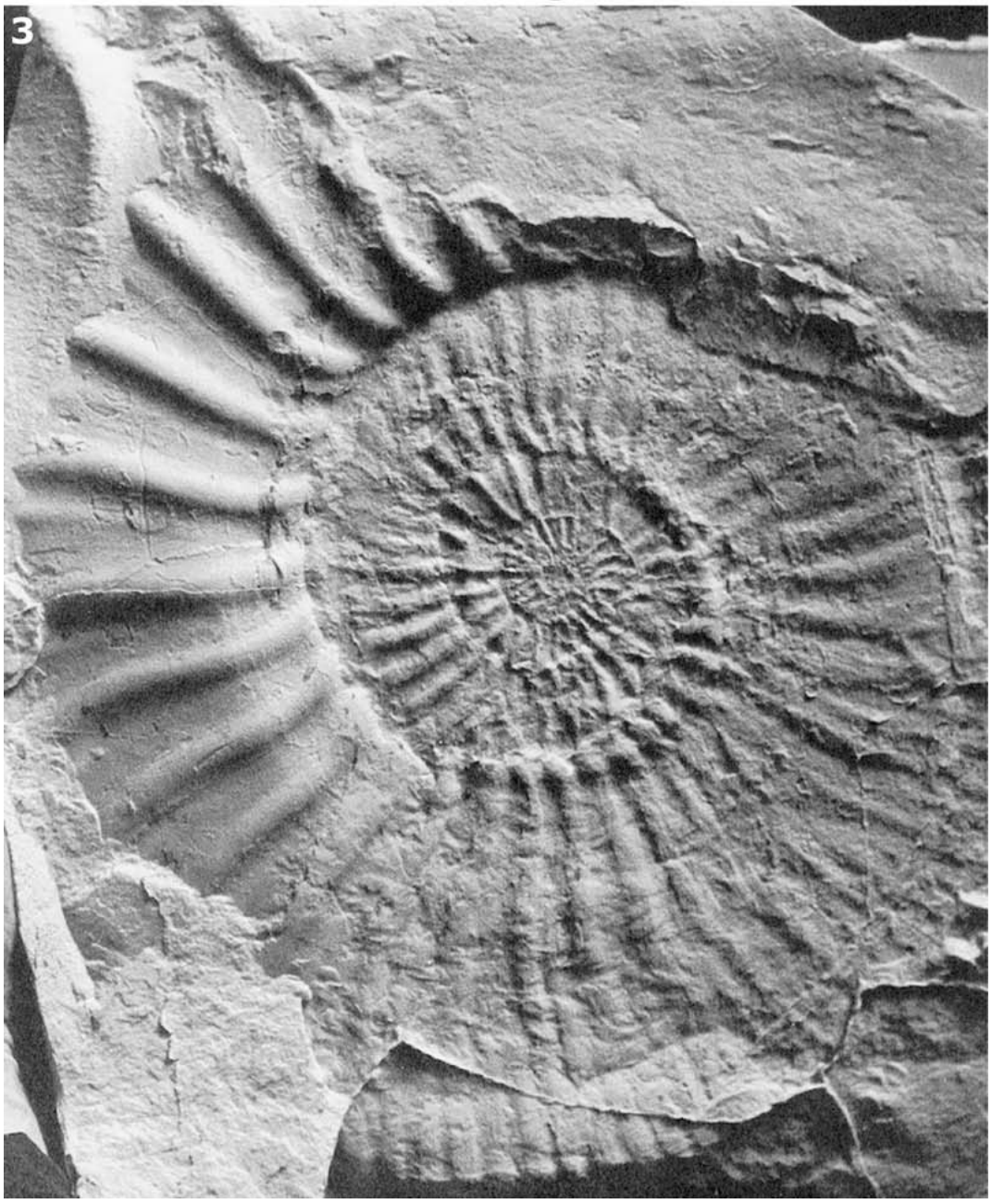
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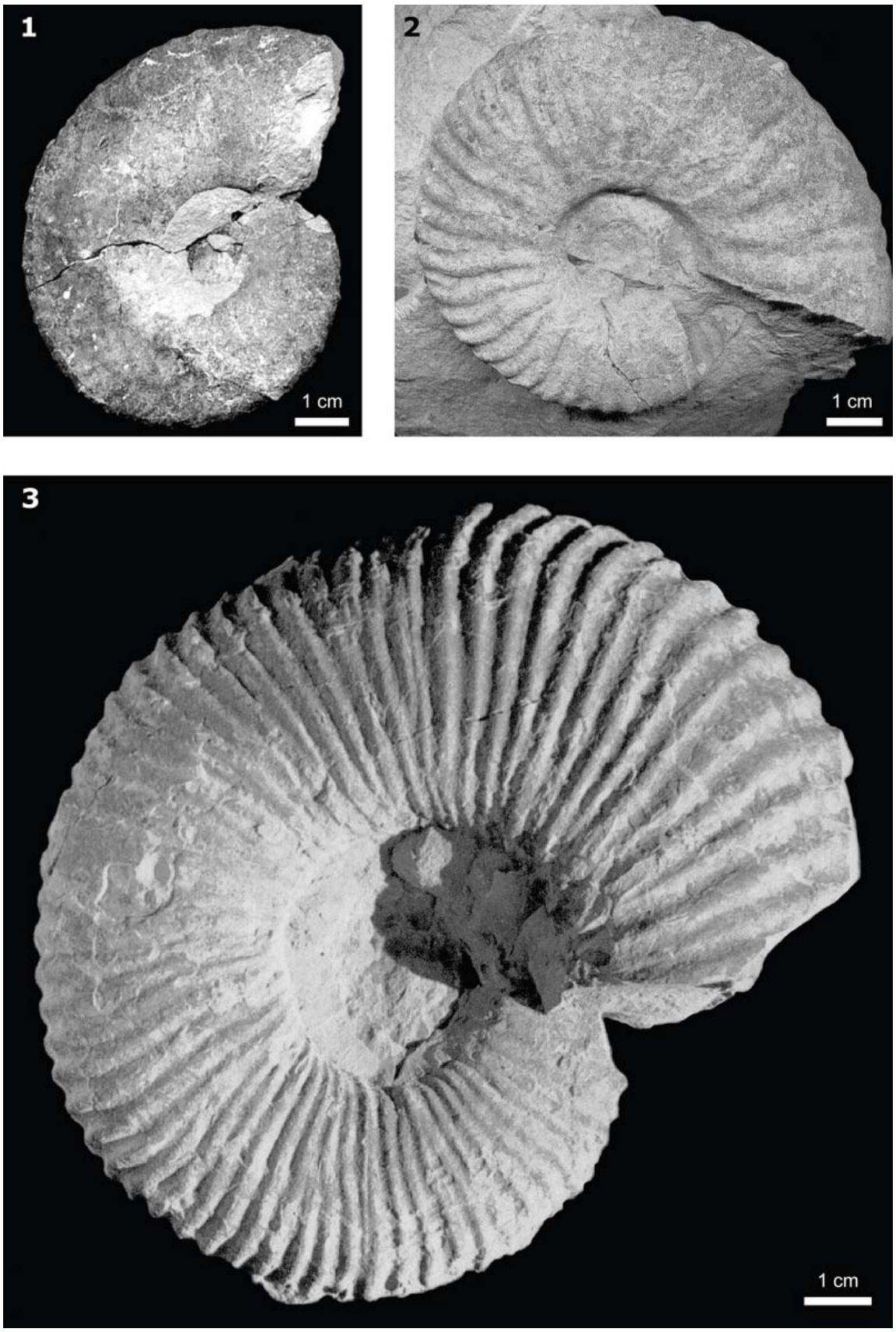

Plate 24:

1) *Parahoplites* sp. n° C.919, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 64.
2) *Parahoplites multicostatus* SINZOW, n° PRA2016, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 78.
3) *Epicheloniceras waageni* (ANTHULA), n° C.920, middle Aptian (Gargasian), Melchioris Zone, La Marcouline section, bed 76.